

**MATE-CHOICE COPYING BEHAVIOUR IN THE GUPPY
(*POECILIA RETICULATA*):**

**COPYING IN THE WILD
AND
THE ROLE OF SOCIAL FAMILIARITY IN COPYING**

By

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ABSTRACT

Behavioural decisions by individuals, while largely independent, are also influenced by social experiences. Mate-choice copying behaviour is an alternative non-independent mating strategy, whereby individuals incorporate the observed mate choice of others into their own mating decisions. The Trinidadian guppy (*Poecilia reticulata*) is one species in which 'observer' females are known to copy the mate choice of 'demonstrator' females under controlled laboratory conditions. As guppies live in mixed-shoals in nature, there are ample opportunities to interact and form social associations with others; thus, one might expect copying to be prevalent. Here, I investigated whether 1) female guppies will mate-choice copy other female conspecifics in their natural riverine habitat in Trinidad, and 2) the social association (i.e. degree of familiarity) between individuals affects their tendency to copy in the laboratory. Despite negative laboratory results which did not reveal copying behaviour, this study is the first to provide empirical evidence for mate copying in guppies in the wild. These field results suggest that mate-choice copying is not simply a laboratory artefact, but is an adaptive alternative mating strategy in this species.

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DEDICATION

~ To my mom, for her tremendous selflessness, her remarkable compassion, and her endless encouragement ~

and

~ To my dad, for his positive outlook, his utmost support, and for his continual belief in me regardless of how crazy I may be ~

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CHAPTER 1

INTRODUCTION

1.1 BACKGROUND

Behaviour in animals tends to vary greatly among species, across populations, within groups, and between individuals. Such behavioural variation is determined by both genetic and environmental factors and their interactions. While there is a strong genetic basis for the evolution and expression of behaviour (Andersson 1994; Kirkpatrick & Dugatkin 1994), one additional, and often overlooked, factor of influence is that of social or cultural mechanisms. The social interactions that occur between individuals, involving anything from simple observation to physical association through group living, shoaling, foraging, territorial defense, and mating, can significantly influence behavioural expression (Brown & Laland 2003). Here, I specifically focus on mating behaviour, which includes social interactions such as mate searching, attraction and competition (Alatalo et al. 1991; Andersson 1994). These socially-mediated interactions influence the mating decisions of individuals (Gibson & Höglund 1992; Pruett-Jones 1992), and consequently warrant attention. Our knowledge of the underlying social forces that influence certain components of mate-choice behaviour is incomplete. Consequently, this thesis attempts to further elucidate the relationship between social associations and mating behaviour, and specifically aims to broaden our understanding of the role of social familiarity among individuals in mate choice and sexual selection.

1.1-1 *Sexual Selection*

Within the context of mating, social interactions are highly prevalent and express themselves in various forms through mate attraction, mate competition and mate choice (Alatalo et al. 1991; Andersson 1994). Depending on their success in attracting and competing for high-quality mates, individuals will differ in their reproductive success. Sexual selection, defined as the differential reproductive success of individuals owing to mate competition and choice, results in the evolution and expression of distinct physical and behavioural traits in populations (Andersson 1994).

Sexual selection theory proposes that female mating preferences act as one of the predominant forces directing the evolution of male secondary sexual characters. For example, a strong female preference for bright body coloration or elaborate ornamentation can select for these specific male phenotypic traits, and cause them to spread within a population (Houde 1987; Kirkpatrick 1987; Pomiankowski 1988; Andersson 1994). Sexually-selected traits may confer a mating benefit to an individual, but often at a survivorship cost. For example, although bright male body colouration may be preferred and thereby selected for by females, males expressing this trait may be more vulnerable to predation and may thus experience reduced survival (Burke 1982; Magnhagen 1991). Depending on the direction and strength of sexual selection, certain traits may be expressed weakly whereas others may be highly pronounced; novel traits may have difficulty invading a population or may rapidly spread, whereas other traits may become entirely suppressed (Kirkpatrick & Dugatkin 1994). While it is known that female mating preferences and male traits have the potential to coevolve (Andersson

1994), it is of particular interest as to how the evolution of these traits in both sexes may be influenced by social associations and interactions among individuals.

1.1-2. Mate Choice

Mate choice strongly directs the prevalence of certain phenotypic traits and sexual selection processes (Andersson 1994). Within populations, the choice of a mate tends to be based predominantly upon both the preferences of individuals of one sex for particular physical or behavioural traits in the other sex (Andersson 1994; Syriatowicz & Brooks 2004) and the sexual responsiveness of those individuals (i.e. their willingness to invest in mate sampling) towards a potential mate (Widemo & Saether 1999; Jennions & Petrie 1997). While mating preferences can have a heritable basis, a considerable degree of variation is maintained in such preferences among individuals (Jennions & Petrie 1997; Widemo & Saether 1999).

Along with the potential benefits of choosing a high-quality mate, there are various fitness costs associated with mating behaviour (Andersson 1994). Individuals invest time and energy in mate searching and assessment, and these activities can pose risks to one's survival (Andersson 1994; Godin & Briggs 1996). In most animal species, it is the female who engages in mate assessment and choice (Andersson 1994; Widemo & Saether 1999; Syriatowicz & Brooks 2004), and is thereby subject to the various costs associated with this endeavour. When independently seeking and assessing a potential mate, females incur time and energy expenditure, predation risk, injury risk, and/or loss of prospective mates to competitors (Pomiankowski 1987; Real 1990; Reynolds & Gross 1990). The guppy (*Poecilia reticulata*) is one example of a species wherein female

preference tends to be based predominantly on male body size, coloration and courtship behaviour (Farr 1989; Godin & Dugatkin 1995; Houde 1997). When mate choice is costly, females often reduce their degree of choosiness accordingly; for example, under increased predation risk, female guppies tend to be less 'selective' and will lower their preference for brightly coloured males (Houde & Endler 1990; Pocklington & Dill 1995; Godin & Briggs 1996). Depending upon the degree of cost, individuals may be constrained in their ability to select an optimal mate (Gibson & Bachman 1992), and may consequently engage in random matings (Pomiankowski 1987). An alternative option to mating indiscriminately involves relying on the knowledge of other individuals. Through the acquisition and use of publicly shared information, females could 'socially learn' about the quality of potential mates from others, and use this information to make future mating decisions (Brown & Laland 2003; Kendal et al. 2005).

1.1-3. Social Learning and Cultural Transmission of Information

Social learning, regarded as the acquisition of novel behaviour or of information through direct observation or interaction with others, can shape the behavioural decisions of individuals and affect their fitness (Brown & Laland 2003; Dall et al. 2005; Kendal et al. 2005). As novel information is socially acquired, learned, and spread through populations and over generations, cultural transmission of behaviour can occur. Information transfer that is culturally based has the potential to spread rapidly throughout populations and may have considerable impacts even within a single generation (Dugatkin 2000). Because independent learning and decision-making can be costly, individuals may rely on public information to acquire knowledge that is relevant to

survival under certain conditions (Dall et al. 2005; Kendal et al. 2005). For example, when faced with the costs associated with independently selecting a high-quality mate, females may rely on other sources (i.e. nearby female conspecifics) for information about male quality in making their own mating decisions.

Although the learner often benefits from social information acquisition, there are also potential behavioural risks associated with learning socially. The information acquired may be inaccurate, and it may originate from an unreliable source (Laland 2004; Dall et al. 2005; Kendal et al. 2005). One can therefore not assume that social learning and the use of socially-conveyed information are always adaptive (Kendal et al. 2005). Instead, individuals experience evolutionary trade-offs when assessing whether to acquire reliable but costly information independently, or to use cheap but potentially less accurate information when learning from others (Dall et al. 2005; Kendal et al. 2005). In exploring the mechanisms underlying cultural information transmission and use, it is important to consider how both the quality of information and the reliability of its source may have an effect on social learning processes and behavioural decision-making.

Recently, much attention has been directed towards the role of social factors and cultural information transmission in mate preference and choice (Gibson & Höglund 1992; Laland 1994; Brown & Laland 2003; Kendal et al. 2005). While traditional evolutionary models of sexual selection commonly assume that female preferences for particular male traits are determined by genetic factors alone (Lande 1981; Andersson 1994; Jennions & Petrie 1997), there is a growing body of evidence supporting a role for social or cultural factors in shaping mating preferences and choice (Gibson & Höglund 1992; Pruett-Jones 1992; Brooks 1996; Dugatkin 1996a). One culturally-based

mechanism used by animals to transmit information is imitation. 'Imitation', a term controversial in its definition, can be described simply as a process whereby a naïve individual mimics or copies the observed behaviour of another individual. More comprehensively, imitation can be viewed not only as a predominant root of social information exchange between individuals, but also as a strong force driving the cultural transmission of behaviour (Dugatkin 2000). George Romanes (1884) was the first to identify and explore the role of imitation in social learning (Dugatkin 2000), and learning through imitation has been studied in many social contexts such as foraging (Zentall & Galef 1988) and aggressive interactions (Oliveira et al. 1998). As imitation may strongly influence female mate-choice decisions, it has the potential to influence sexual selection processes, and thereby warrants attention.

1.1-4. *Mate-Choice Copying*

Imitation was first explored in the context of mate choice by Bradbury & Gibson (1983) and Bradbury et al. (1985). Their studies on lekking grouse drew attention to a high variability in male mating success which could not be explained by independent female choice alone. Wade and Pruett-Jones (1990) later followed up on this observation by modeling the influence of female mate-copying behaviour on male mating success. This mechanism of imitating the mate choice of others, defined as 'mate-choice copying', has been more recently recognized as a form of social learning (Gibson & Höglund 1992; Pruett-Jones 1992; Dugatkin 1996a; Westneat et al. 2000). Mate-choice copying occurs when one female (the 'observer') has the opportunity to directly observe another female conspecific (the 'demonstrator') consorting with potential mates, and when the observer

female subsequently uses this socially-acquired information in choosing mates (Dugatkin 1996a; Briggs et al. 1996; Westneat et al. 2000). Copying the mate choice of other individuals is one mechanism whereby females can presumably acquire locally-adaptive behaviour with regards to male quality, and reap the benefits of mating with high-quality males, without incurring the costs associated with independent mate searching, discrimination, and choice (see 1.1-2) (Wade & Pruett-Jones 1990; Pruett-Jones 1992; Gibson & Höglund 1992; Dugatkin 1992, 1996a; Dugatkin & Godin 1993, 1998a; Brown & Laland 2003).

Mate-choice copying is regarded as a socially-mediated, alternative non-independent mate-choice strategy, which results from social learning (Gibson & Höglund 1992; Westneat et al. 2000). The adaptive significance of copying will likely depend upon the relative costs and benefits associated with actively choosing a mate, and on a female's ability to differentiate between males (Real 1990; Pruett-Jones 1992). Females are most likely to engage in mate-choice copying either when a) the fitness costs of mate sampling and assessment outweigh the associated benefits, b) they are in poor condition or highly vulnerable to sampling costs, or c) they are unable to gain enough information about potential mates independently (Gibson & Höglund 1992; Pruett-Jones 1992; Dugatkin 1998). These factors will vary within and among years depending on ecological and environmental conditions, with female age and condition, and with male traits and behaviour (Losey et al. 1986; Pruett-Jones 1992; Dugatkin & Godin 1998a,b). Upon choosing to copy, however, copiers also face the risk of mating with poor-quality males; as demonstrator females may have made errors in mate discrimination, recently-mated

males may be depleted in their sperm supply (Gibson and Höglund 1992; Dugatkin & Godin 1993; Dugatkin 1996a; Westneat et al. 2000).

Mate-choice copying behaviour has been documented mainly in species with polygamous or promiscuous mating systems (Gibson & Höglund 1992; Höglund & Alatalo 1995), including a variety of species of birds such as the sage grouse, *Centrocercus urophasianus* (Gibson et al. 1991), the black grouse, *Tetrao tetrix* (Höglund et al. 1995), and the Japanese quail, *Coturnix c. japonica* (Galef & White 1998), and species of fish including the sailfin molly, *Poecilia latipinna* (Schlupp et al. 1994; Schlupp & Ryan 1997; Witte & Ryan, 1998), the Japanese medaka, *Oryzias latipes* (Grant & Green 1996), the whitebelly damselfish, *Amblyglyphidodon leucogaster* (Goulet & Goulet 2006), the ocellated wrasse, *Symphodus ocellatus* (Alonzo 2008), and the guppy, *Poecilia reticulata* (Dugatkin 1992, 1996a, 1998; Dugatkin & Godin 1992, 1993; Briggs et al. 1996).

1.2 STUDY OBJECTIVES

Although mate-choice copying behaviour has received considerable theoretical and empirical attention and has been documented in a number of species, its underlying mechanisms are not well understood. As such, I chose to investigate two formerly overlooked aspects of mate-choice copying behaviour using the guppy as a study species. Firstly, I ascertained whether female guppies mate-choice copy under natural conditions in the wild. Secondly, I tested experimentally whether the degree of social familiarity between demonstrator and observer females affected the latter's tendency to mate-choice copy under controlled laboratory conditions.

1.2-1. *Study Species*

Using the guppy as a study species, Dugatkin (1992) and Dugatkin and Godin (1992) were the first to report experimental evidence for female mate-choice copying in any species. As a highly promiscuous poeciliid fish, the guppy undergoes internal fertilization and exhibits a non-resource based mating system. Adult males repeatedly court females using sigmoid displays, but will also attempt 'sneak' copulations in the absence of female consent (Farr 1989; Houde 1997; Pilastro & Bisazza 1999). Over the duration of their lifetime, individual females will undergo multiple male matings (Kelly et al. 1999). In nature, the guppy lives in mixed-sex shoals, wherein opportunities for females to observe other females choose mates presumably occur, and wherein females can readily form social associations with other individuals (Houde 1997; Magurran 2005). Owing to its promiscuous mating system (Houde 1997; Kelly et al. 1999), shoaling in mixed-sex groups in nature (Houde 1997; Magurran 2005), and known mate-choice copying in the laboratory (Dugatkin 1992; Dugatkin & Godin 1992, 1993; Dugatkin 1996b, 1998; Briggs et al. 1996), I have used the Trinidadian guppy as my study species.

1.2-2. *Mate-Choice Copying in the Wild*

There is fairly extensive evidence for mate-choice copying behaviour in the guppy under laboratory conditions (refs. loc. cited); however, whether guppies exhibit mate-copying behaviour under natural conditions in the wild is unknown. In accordance with theory, one would expect mate-choice copying to be prevalent among wild guppies, particularly when the costs associated with independent mate searching and selection are

high. My first aim was to experimentally test for mate-choice copying behaviour among wild guppies in their natural habitat in the Quaré River, Trinidad. One objective of this work was to ascertain whether and to what degree mate-choice copying is exhibited in the wild, and to what extent our current knowledge of mate-copying behaviour, observed under laboratory conditions, is compatible with that exhibited in the wild. Knowing whether female guppies will copy other female conspecifics in the wild is relevant to better understand the prevalence of this behaviour in nature and to better interpret its ecological and evolutionary significance.

1.2-3. Mate-Choice Copying and Social Associations

Within the context of mate choice, it remains uncertain whether and to what degree social associations between individuals influence one's decision to learn asocially (i.e. independently) or to engage in social learning activities (i.e. mate-choice copying). While mate copying is known to occur in a number of species (reviewed in Gibson & Höglund 1992; Dugatkin 1996a; Westneat et al. 2000), the underlying mechanisms shaping whether females will engage in copying behaviour remain less well understood. Because cultural factors likely influence such decision-making processes, I chose to investigate the role of social association between demonstrator and observer females in mate-choice copying behaviour.

Individuals of many species possess the cognitive ability to recognize other individuals, and will often preferentially choose to interact with these 'known' individuals when shoaling, foraging, and in antipredator defence (Griffiths 2003). In fishes, the preferred social association that occurs between individuals following a

previous interaction can be referred to as 'social familiarity' (Ward & Hart 2003). Various benefits are often accrued through associating with socially familiar individuals; by shoaling with social familiars, individuals benefit from enhanced social learning (Swaney et al. 2001), increased foraging success (Ward & Hart 2005), reduced predation risk (Chivers et al. 1995), and reduced competition for resources (Barber and Wright 2001). However, to my knowledge, whether social familiarity plays a role in mate-choice behaviour has not hitherto been addressed.

There is some evidence that individuals will relate the quality and the reliability of information with the origin and identity of its associated source (Laland 2004). Public information obtained from a nearby familiar individual will potentially be considered of higher quality and reliability than that received from an unfamiliar individual (Swaney et al. 2001; Griffiths 2003; Ward & Hart 2003). In the context of mate choice, observer ('focal') females may therefore be more inclined to rely on the information acquired from demonstrator ('model') females and copy the mate preference of these individuals when model females are social familiars than non-familiars.

Specifically, I evaluated whether and to what degree a female's decision to mate-choice copy is related to the identity of the source from which the information was socially acquired. I assessed whether the tendency of an observer female to copy the mate choice of other nearby females was influenced by her prior social affiliation with a demonstrator female who she had recently observed consorting with a male as a potential mate. Based on prior knowledge of the importance of familiarity in the formation of preferred social associations (Chivers et al. 1995; Barber & Wright 2001; Swaney et al. 2001; Griffiths 2003; Ward & Hart 2005), I predicted that females would be more likely

to copy, and would more strongly copy, the (apparent) mate choice of socially-familiar model females than of non-familiar models. Understanding the underlying social mechanisms of mate-choice copying behaviour is of particular relevance, as cultural transmission via copying may influence the nature and direction of sexual selection within populations and across generations (Wade 1979; Wade & Pruett-Jones 1990).

Both components of my study, namely, investigating mate-choice copying behaviour in the wild and the role of social familiarity in mate copying in the laboratory, aim to contribute to a better understanding of the prevalence and generality of this behaviour in nature and of the underlying mechanisms of social information transmission and learning associated with mate copying.

CHAPTER 2

MATE-CHOICE COPYING IN FREE-RANGING TRINIDADIAN GUPPIES

2.1. INTRODUCTION

Mate-choice copying is a socially mediated-behaviour that involves females choosing mates based on their previous observation of the mate choice of other female conspecifics (Gibson & Höglund 1992; Dugatkin 1996a; Westneat et al. 2000; Godin et al. 2005) (see Chapter 1). In theory, this behaviour is likely to be expressed particularly when the costs associated with independent mate searching and assessment are high (Wade & Pruett-Jones 1990; Pruett-Jones 1992; Gibson & Höglund 1992; Dugatkin 1998). There is well-documented evidence for mate-choice copying in several species of polygynous birds and polygynous fishes (see Chapter 1), including the guppy (Dugatkin 1992, 1996a, 1998; Dugatkin & Godin 1992, 1993). Despite studies that provide support for mate copying in the guppy, the majority of work has been done in the laboratory and there has been little to accredit its occurrence in the wild. Empirical evidence for the occurrence of mate-choice copying in the wild is currently available for only three species of fish (Witte & Ryan 2002; Goulet & Goulet 2006; Alonzo 2008) and one bird species (Höglund et al. 1995). There is, however, strong reason to believe that mate-choice copying behaviour ought to be prevalent in nature, particularly in polygynous and promiscuous species.

Dugatkin (1992) and Dugatkin & Godin (1992) were the first to report controlled experimental evidence for female mate-choice copying in the guppy in the laboratory, and several additional studies have since demonstrated copying in female guppies under

laboratory conditions (e.g. Dugatkin 1992, 1996b, 1998, 2007; Dugatkin & Godin 1992, 1993, 1998a; Briggs et al. 1996; Amlacher & Dugatkin 2005; Godin et al. 2005; Vukomanovic & Rodd 2007). It has yet to be determined, however, whether female guppies mate-choice copy in the wild. Consequently, the current field study was carried out to ascertain whether mate-choice copying is also expressed in free-ranging guppies in nature. Although there is evidence that female choice is largely driven by inherent preferences for particular male phenotypic traits in the guppy (Godin & Dugatkin 1995; Dugatkin 1996b; Houde 1997), copying is expected to occur in nature as guppies are promiscuous and live in mixed-sex shoals, wherein sexual interactions are frequent (Houde 1997; Magurran 2005). In such a social context, female guppies receive an abundance of social cues from sighting other nearby matings, which potentially inform them of male quality.

Accordingly, I investigated whether or not free-ranging female guppies socially affiliate and consort with males in a manner consistent with mate-choice copying in their natural riverine habitat in Trinidad. The current study was designed to experimentally test in the field whether patterns of mate-choice copying exhibited by the guppy in the laboratory also occur in the wild. I used a protocol similar to that outlined by Witte & Ryan (2002) in their study examining mate-choice copying in the sailfin molly in nature. The importance of testing whether females mate-choice copy in the wild stems from a desire to better understand the overall generality and relevance of this behaviour, and to identify the conditions under which it occurs in nature.

2.2. METHODS

2.2-1. *Study Species*

The guppy is a species of poeciliid fish that exhibits a highly promiscuous mating system, undergoes internal fertilization, and is live-bearing, but does not exhibit parental care. Adult males repeatedly court females using sigmoid displays, but will also attempt 'sneak' copulations in the absence of female consent (Farr 1989, Houde 1997, Pilastro & Bisazza 1999). When given the opportunity to choose, females select mates based on their phenotypic and behavioural traits, such as bright body colouration, large body size and tail length, and elaborate courtship displays (Farr, 1989; Houde & Endler, 1990; Godin & Dugatkin 1995; Houde 1997). In nature, guppies live in mixed-sex shoals wherein individuals can form social associations with others, and wherein females can presumably observe other females consorting with and selecting males as mates (Houde 1997; Magurran 2005). This type of social system presents a setting in which mate-choice copying is expected to occur.

2.2-2. *Study Site*

Field experiments were conducted in the Quaré River, Trinidad, West Indies (10°41'25"N, 61°11'51"W) between April 14 and 22, 2008. Guppies descended from adults collected from this river are known to copy the mate choice of other females in the laboratory, when given the opportunity to do so (Briggs et al. 1996; Dugatkin 2007). A series of 18 pools were selected from 3 separate sites (6 pools per site) along a 2-km section of the Quaré River. Pools with shallow water and low water flow velocity were chosen, such that the test apparatus could be securely positioned on the substratum near

the shoreline. Trials were conducted daily at one of the three sites, and each site was visited on two occasions, separated by a minimum of 48 hours. At a given site, all of the 6 pools selected were visited twice daily, once in the morning and once in the afternoon, at which times one of either randomly selected '*Experimental*' or '*Control*' Treatments was carried out (see below).

2.2-3. *Experimental Apparatus*

The apparatus consisted of two identical Plexiglas aquaria (25 cm x 10 cm x 20 cm; L x W x H) that were constructed as mirror images when positioned facing one another (Fig. 2-1). Each tank was partitioned into two equal compartments by a solid transparent divider (12 cm x 10 cm x 20 cm). Both the back and side walls of each aquarium were made of solid opaque Plexiglas, whereas the front wall of each was perforated and transparent to allow for both the exchange of visual and chemical cues between stimulus, model, and subject individuals. An additional opaque partition could be inserted into the rear section of either tank, thereby selectively hiding the 'pseudo-model' female from the view of subject females, as necessary.

Prior to the onset of a trial, both aquaria were placed on the substratum in shallow water (10 - 18 cm high), facing one another and in close proximity (mean \pm SE = 72.0 \pm 4 cm) to the shoreline. Tanks were positioned approximately 20 cm apart, forming a corridor between them through which the subject females could swim, view, and approach the stimulus fish freely.

2.2-4. *General Protocol*

Experiments were designed to evaluate the mate preference of free-swimming adult female guppies and to ascertain whether they chose to associate with a stimulus male seen adjacent to and interacting with a model female or with a stimulus male seen alone (placed next to a pseudo-model female hidden from subject females). I compared the total number of subject females that visited a lone stimulus male versus the number that visited a male positioned next to a model female during a 20-min *Experimental* trial, as a measure of mate preference. A female was considered to have mate-choice copied if she chose to visit the stimulus male adjacent to the model female. To further confirm behaviour as being sexually motivated, *Control* trials were conducted to assess whether subject females chose to associate with a stimulus female viewed alone (one individual) or with a stimulus female seen associating with a model female (two individuals). Preference for two females over one would be suggestive of shoaling behaviour.

Fish that were used as stimulus and model individuals were captured using a beach seine net in the early morning of each day of the study prior to trials. Fish were collected from locations in the Quaré River away from any of the study pools. The captured fish were placed in buckets of aerated river water, from which they were selected for trials. At the end of each day, any fish remaining in buckets were released into the river.

The study comprised matched *Experimental* ($N = 36$) and *Control* ($N = 36$) trials. For the *Experimental Treatment*, stimulus males were selectively paired and visually matched both for body length and body colouration, such that the two individuals did not significantly differ in either of these traits. This close matching of males should promote

mate-copying in females (Gibson & Höglund 1992; Kendal et al. 2005), because the similarity in phenotype between the paired males would likely render independent mate assessment and choice by females difficult. Work by Dugatkin (1996b) has shown that when guppy males differ in orange body colouration by only 12% and 24%, females relied on copying the mate choice of other females. Similarly, for the *Control Treatment*, stimulus females were paired and matched for body size within each trial, to control for the potential bias of subject females choosing to associate with either the larger or smaller stimulus fish.

For each trial within both *Experimental* and *Control Treatments*, model and pseudo-model females were also paired and closely matched for body size. This was done to control for any potential bias that may stem from differential activity of stimulus fish or model fish. For example, it is possible that stimulus males (*Experimental Treatment*) or stimulus females (*Control Treatment*) may be inclined to court or interact to a different extent with model or pseudo-model individuals when the sizes of these fish differ significantly. For the *Experimental Treatment*, the average (\pm SE) body length of model female (29.6 ± 1.0 mm) and pseudo-model female (29.9 ± 0.96 mm) did not significantly differ (*Wilcoxon matched-pairs test*: $Z= 1.648$, $P= 0.099$, two-tailed). Similarly, for the *Control Treatment*, there was no significant difference (*Wilcoxon matched-pairs test*: $Z= 0.376$, $P= 0.707$, two-tailed) in the average (\pm SE) body lengths of model females (28.2 ± 0.99 mm) and pseudo-model females (28.1 ± 0.94 mm).

Within a Treatment, paired stimulus fish (either males or females) were placed facing one another in each tank, in opposite compartments situated nearest to the shore. A paired model or pseudo-model individual was placed adjacent to the stimulus fish in the

remaining compartment of each tank that was positioned furthest from the shore (Fig. 2-1). An opaque partition was inserted into the section of the tank holding the pseudo-model female, to hide this individual from the view of subject fish swimming in the corridor between the two tanks. The purpose of the pseudo-model was to control for stimulus fish activity, such that the adjacent stimulus fish would behave similarly to the stimulus fish situated next to the model female. The initial position of the model and pseudo-model females (on either the left or right side of the observer) was randomly selected and alternated between *Experimental* and *Control Treatments*.

Once fish were positioned in the apparatus, an initial 10-min preference test began when the first subject female swam through the corridor and visited either of the two stimulus fish. During this time, the number of subject females visiting the stimulus fish next to the model and the number of subject females visiting the stimulus fish next to the pseudo-model were recorded separately. Subject females were counted when they entered the corridor from either of its entry sides, and when they were within one body length of the tank in front of and behaviourally interacting with the first visited stimulus fish (Fig. 2-1). When females entered as a group of several individuals, only the first individual was counted when visiting a stimulus fish. Only when females had exited and re-entered the corridor could they potentially be counted again as subject females. After this first test, the positions of the stimulus fish were switched to control for any potential side biases of approaching subject females, and a second similar 10-min preference test was then conducted. Following each trial, stimulus and model individuals were measured for total body length, and then released back into the river. Within a pool, a matched pair of *Experimental* and *Control* trials were conducted daily, the order of which randomized.

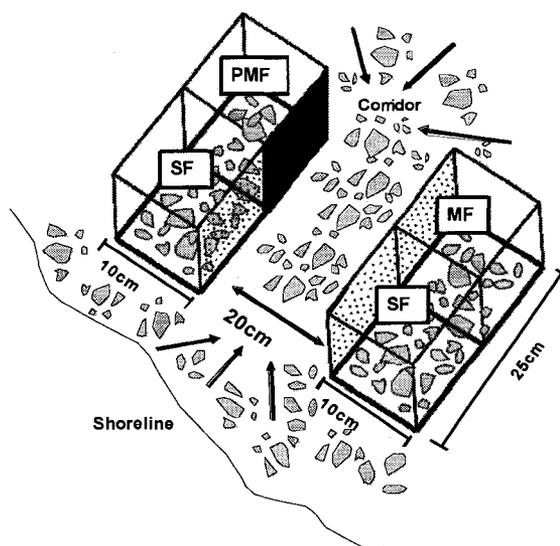


Figure 2-1: Overhead view of the experimental apparatus. Tanks were identical as mirror images, with solid outer opaque siding and transparent perforated inner walls facing the central corridor. In the *Experimental* treatment, stimulus fish (SF) were males, and in the *Control* treatment stimulus fish were females. A model female (MF) and a pseudo-model female (PMF) were each placed adjacently to one of the two stimulus fish, in compartments located furthest from the shoreline. During trials, the pseudo-model female was kept hidden from subject fish in the corridor by an opaque partition. Female preference was quantified by counting the number of subject females that entered the corridor from either side (denoted by arrows), approached either stimulus fish within one body length of its compartment, and interacted behaviourally with the latter.

2.2-5. *Experimental Treatment: Testing for female mate-choice copying*

For the *Experimental* trials, stimulus males were paired and visually matched for body length and body colouration. Post-hoc statistical analyses indicated that the total body lengths of paired stimulus males did not differ on average (\pm SE) (male 1 = 20.7 ± 0.73 mm, male 2 = 20.5 ± 0.75 mm; *Wilcoxon matched-pairs test*: $Z= 0.678$, $P= 0.498$, two-tailed). Colour matching of males was conducted by eye, so as to avoid imposing any additional stress on the fish that may have arisen from excessive handling or photographing. This involved pairing two individuals that were similar in the amount of total body area covered in orange and black spots. From my prior laboratory experience with visual colour-matching of males (confirmed with digital photographs) from this population, I am confident that paired stimulus males used in the current study did not differ significantly in total body colouration.

Within this Treatment, paired males were used as stimulus fish to ascertain whether subject females entering the corridor would preferentially associate with a male that was observed adjacent to a model female or with a male adjacent to a pseudo-model female (apparently alone). For a given trial, paired males were placed in opposite compartments, each adjacent to either a paired model or pseudo-model female. Two 10-min preference tests were conducted, with the position of stimulus males switched between tests. For each test, I observed and recorded the number of free-ranging subject females visiting both the stimulus male next to the model and the stimulus male next to the pseudo-model. The total number of subject females observed within one body length and interacting with either stimulus male during a 20-min trial was taken as a measure of mate attraction by the subject females toward the stimulus males. An observed preference

for the stimulus male adjacent to the model female was considered to be consistent with mate-choice copying (cf. Dugatkin 1992; Dugatkin & Godin 1992, 1993).

2.2-6. *Control Treatment: Controlling for female shoaling behaviour*

A *Control Treatment* was carried out to confirm that any preferences for stimulus males exhibited by subject females in the *Experimental* trials were attributable to females being sexually motivated and not simply the result of shoaling with other individuals. This was accomplished by using an identical protocol to the *Experimental Treatment* described above, but with one notable difference; the stimulus males were replaced with stimulus females (to remove the sexual context of choice). Paired model and pseudo-model females were similarly placed adjacently to stimulus females and opposite to one another in compartments furthest from shore. Whereas subject females were expected to show a preference for males that were adjacent to a model in the *Experimental Treatment*, no such preference was expected in the *Control Treatment*. Instead, if subject females were not shoaling (i.e. did not prefer to affiliate with two fish over one), there should be no difference in the number of females visiting the stimulus fish next to a model (i.e. associating with two females) and the number visiting the stimulus fish next to a pseudo-model (i.e. associating with one female)

In the *Control Treatment*, stimulus females were similarly matched for body size, such that on average (\pm SE) the total body lengths of paired stimulus female 1 (27.0 ± 0.87 mm) and stimulus female 2 (27.2 ± 0.89 mm) did not differ significantly (*Wilcoxon matched-pairs test*: $Z= 0.974$, $P= 0.33$, two-tailed). For a given trial, two 10-min preference tests were conducted, with the position of stimulus females switched between

tests to control for any potential side biases. In each test, I observed and recorded the number of subject females visiting both the stimulus female next to the model and the stimulus female next to the pseudo-model (apparently alone).

2.2-7. *Statistical Analyses*

Since it was possible, although unlikely, that a subject female entering the corridor was counted visiting a stimulus fish on more than one occasion, I did not statistically compare the total number of subject fish associating with either stimulus fish within each trial. Instead, the *Binomial test* was first applied to compare the total number of trials in which the majority of subject females visited the stimulus fish adjacent to the model versus the number of trials in which the majority visited the apparently alone stimulus fish (adjacent to the pseudo-model). This was done for both the *Experimental* and *Control Treatment* separately. The aforementioned frequency data, obtained for the *Experimental* and *Control* trials, was then compared using the *Fisher exact test*.

Secondly, for both the *Experimental* and *Control* trials separately, I compared the mean number of females that visited the stimulus male (or female) next to the model versus the mean number that visited the lone stimulus male (or female) using the *Wilcoxon matched-pairs signed-ranks test*. Across Treatment comparisons were also conducted using the *Wilcoxon matched-pairs test* to assess whether the relative number of females visiting the stimulus fish (stimulus male in the *Experimental treatment* and female in the *Control Treatment*) varied significantly. This was done to validate the results found within *Experimental* and *Control Treatments*, and to further distinguish the observed fish behaviours as being either sexually motivated or a shoaling response.

2.3. RESULTS

2.3-1. *Experimental Treatment*

More subject females were attracted to and associated with the stimulus male next to the model female than with the other (paired) stimulus male in 34 out of 35 trials (*Binomial test*: $P < 0.0005$; Fig. 2-2a). In one trial, an equal number of subject females visited the stimulus male with the model female and the stimulus male with the pseudo-model female. This observed preference pattern for the stimulus male next to the model female in the experimental trials is significantly different (*Fisher exact test*: $P = 0.00002$) from the pattern of social associations exhibited by the subject females in the control trials (Fig. 2-2a).

On average (\pm SE), there were significantly more subject females (17.9 ± 1.84) that chose to associate with the stimulus male next to the model female than females (7.2 ± 0.98) that associated with the single stimulus male (*Wilcoxon matched-pairs test*: $Z = 4.976$, $P < 0.0005$, two-tailed; Fig. 2-2b).

2.3-2. *Control Treatment*

In the *Control Treatment*, subject females did not show any preference for associating with either two visible females (stimulus female next to visible model) or one visible female (stimulus female next to hidden pseudo-model). Subject females entering the corridor associated with the stimulus female next to a model in only 17 out of 32 trials, which is not significantly different from chance (*Binomial test*: $P = 0.50$; Fig. 2-2a). In 4 out of the 36 trials, an equal number of females visited the stimulus female next to the model and the single stimulus female. Overall, there was no significant difference

(*Wilcoxon matched-pairs test*: $Z= 0.122$, $P= 0.903$, two-tailed; Fig. 2-2b) in the mean (\pm SE) number of subject females (17.6 ± 2.41) that associated with the stimulus female adjacent to the model and females (17.1 ± 2.20) that visited the stimulus female next to the pseudo-model. Subject females thus exhibited no preference for associating with either one female or two females, suggesting that they were not shoaling per se. Instead, this result suggests that the behaviour observed in the *Experimental Treatment* (wherein females displayed a strong preference for the male adjacent to a model female) was sexually motivated as opposed to being an effect of shoaling. Consequently, I can conclude that in the *Experimental Treatment* subject females were in fact 'mate-choice copying' the apparent mate choice of other nearby female conspecifics.

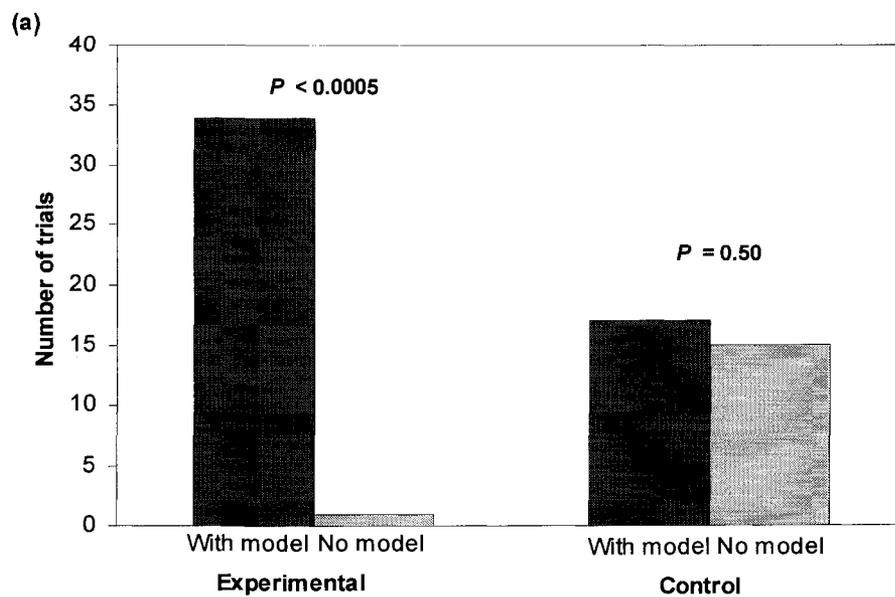


Figure 2-2: (a) Number of trials in which more subject females associated with the stimulus fish (stimulus male in the *Experimental Treatment* and stimulus female in the *Control Treatment*) seen adjacent to the model versus the stimulus fish that was (apparently) alone. *P-values* shown were obtained using the *Binomial test*.

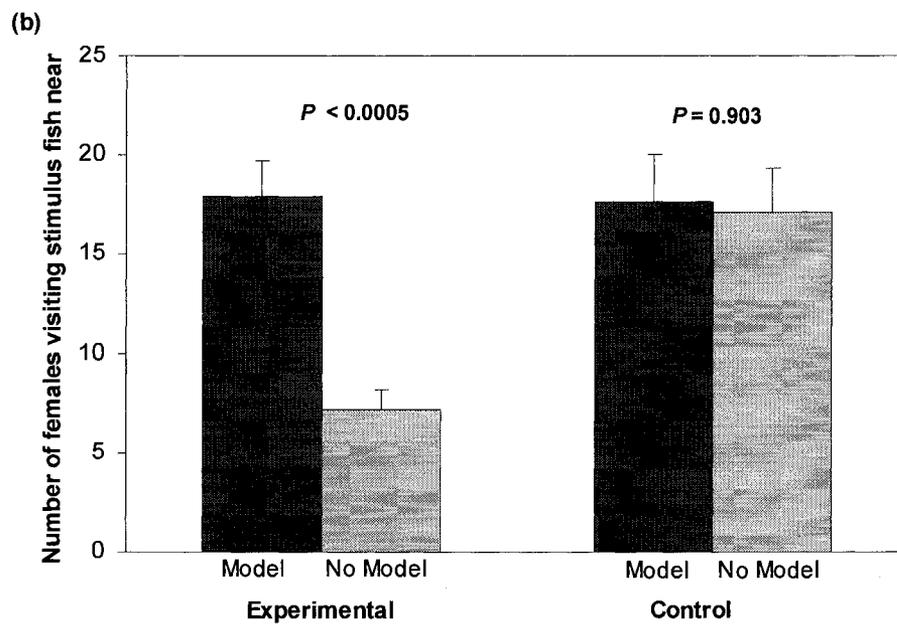


Figure 2-2: (b) Mean (+ SE) number of subject females visiting the stimulus male (*Experimental Treatment*) or stimulus female (*Control Treatment*) seen adjacent to a model female or the stimulus fish that was seen alone. *P-values* shown were obtained using the *Wilcoxon matched-pairs test*.

2.3-3. Across-Treatment Comparison

To further strengthen the within-Treatment results obtained, additional analyses were conducted to compare the relative number of females visiting the stimulus fish (male or female) next to a model fish across *Experimental* and *Control Treatments*. There were relatively more (*Wilcoxon matched-pairs test*: $Z= 4.823$, $P< 0.0005$, two-tailed) females ($72.7 \pm 2.16\%$) attracted to the stimulus male adjacent to a model female in the *Experimental Treatment* than females ($50.9 \pm 1.79\%$) attracted to the stimulus female next to a model female in the *Control Treatment* (Fig. 2-3). Subject females thus exhibited a preference for males observed near a model female (sexual context present) but not for females observed near a model female (sexual context absent). This result further supports the conclusion that females were ‘mate-choice copying’ and not simply shoaling.

Additional across-Treatment comparisons indicate that on average a greater number of females entered the corridor in the *Control* trials (34.7 ± 4.47) than in the *Experimental* trials (25.1 ± 2.54). However, this difference was not statistically significant (*Wilcoxon matched-pairs test*: $Z= 1.713$, $P= 0.087$, two-tailed), and may have simply been a random effect of the time of day, solar or weather conditions, or the sampling location.

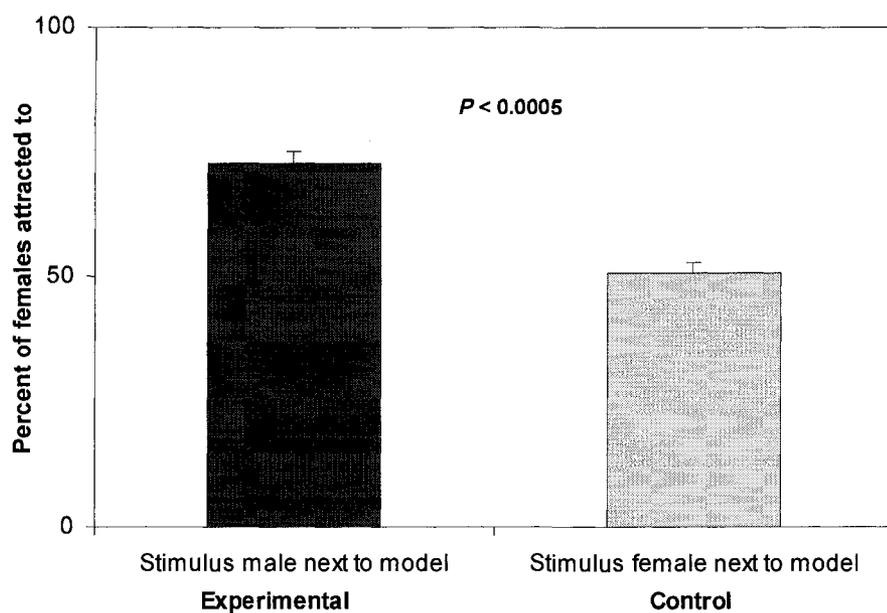


Figure 2-3: Mean (+ SE) percentage of subject females observed associating with the stimulus fish adjacent to the model female (out of all females visiting both stimulus fish in a given trial) for the *Experimental* and *Control Treatments* separately. *P-value* shown was obtained using the *Wilcoxon matched-pairs test*.

2.4. DISCUSSION

Although mate-choice copying behaviour has been widely documented for a variety of species (see Introduction above and Chapter 1), very few studies have reported evidence for this behaviour in the same species both in a laboratory and in the wild. Witte and Ryan (2002) were the first to demonstrate mate-choice copying in the sailfin molly in both of these contexts. Two additional recent studies provide empirical evidence showing that female whitebelly damselfish (*Amblyglyphidodon leucogaster*) and ocellated wrasse (*Symphodus ocellatus*) can copy the mate choice of other nearby females in their natural coral reef habitats (Goulet & Goulet 2006; Alonzo 2008). For the guppy, there is ample evidence indicating that females will mate copy under laboratory conditions (refs. loc. cited); however, the current field study is the first to report behaviour that is consistent with mate-choice copying by female guppies in the wild. My results clearly indicate that, when given the opportunity, wild female guppies will preferentially associate with males that are observed adjacent to a model female than with apparently lone males, a behaviour which is consistent with mate-choice copying. Other studies have shown that the mating preferences exhibited by female guppies strongly correlate with their actual choice of mate, when mating is allowed (Bischoff et al. 1985; Dugatkin & Godin 1992; Kodric-Brown 1993). Therefore, I used the aforementioned female preference criterion as an indicator of mate choice.

The *Experimental* results obtained here in support of mate-choice copying are further strengthened by the *Control Treatment*, wherein there was no indication that the observed behaviour of females reflected shoaling. Rather, subject females did not on average display a preference for associating with either one female or two females; they

were thus not shoaling with other individuals. I therefore conclude that the behaviour of the subject females observed in the *Experimental Treatment* (Figs. 2-2 & 2-3) was not simply a shoaling response, but rather a sexually-motivated mating preference for males observed near and interacting with another female (the model), thus consistent with mate-choice copying behaviour.

Several functional explanations have been advanced for the occurrence of mate-choice copying behaviour. One possible fitness benefit of copying is that it may reduce the costs typically associated with independent mate searching (Wade & Pruett-Jones 1990; Dugatkin 1992; Pruett-Jones 1992; Gibson & Höglund 1992). In independent mate choice, a significant amount of time and energy is expended by females in searching for males and assessing their quality while at the same time evading predation (Lima and Dill 1990; Pomiankowski 1987; Magnhagen 1991; Sih, 1994; Dugatkin & Godin 1998b). With individual mate assessment also comes the risk of discrimination errors, particularly when females are young and inexperienced (Dugatkin & Godin 1993; Westneat et al. 2000). As a result, females may selectively circumvent some of these costs and risks by relying on the observed mate assessment and choice of other nearby female conspecifics. As discussed in more detail in Chapter 1, while mate-choice copying behaviour can be beneficial under certain circumstances, it does not exist free of its own costs. In copying others, there is always the possibility that copiers will mate with poor-quality males, that model females may have made errors in discriminating between males, or that the already-mated and preferred males may be depleted in sperm supply (Pomiankowski 1987; Gibson and Höglund 1992; Dugatkin 1996a).

With evidence for mate-choice copying in the guppy under natural conditions provided here, it is interesting to speculate as to why this behaviour might be expressed and maintained within a population. One possibility is that mate copying may be selected for under specific environmental conditions. The Quaré River is a site of high predation pressure on guppies; this river contains high densities of several fish predators, including the pike cichlid (*Crenicichla alta*), blue acara cichlid (*Aequidens pulcher*) and the characin (*Astyanax bimaculatus*) (Endler 1978, 1983; Godin 1995). This predation pressure may present a setting in which it is hazardous for female guppies to independently search for and assess potential mates. Other studies have shown that, under high predation risk, females will modify their behaviour accordingly by reducing both their preference for particular male traits (e.g. bright body colouration) and their overall sexual activity level (Godin & Briggs 1996). Under high predation threat, one might therefore expect females to rely more heavily on publicly-acquired information of male quality received from other females when selecting a mate than on independent mate choice. Correspondingly, there is evidence that female guppies will exhibit mate copying behaviour when in the presence of predators (Briggs et al. 1996). This is one mechanism whereby mate-choice copying could potentially have become prevalent and spread throughout a population, as it might serve as an alternative adaptive strategy for survival and reproduction.

Copying behaviour may also be favoured in this type of environment, as guppy densities tend to be relatively high in the Quaré River (e.g. on average 13 adult guppies per m², Godin 1995; personal observation). Under controlled experimental conditions wherein individuals are not exposed to external social influences, female guppies exhibit

'inherent' mating preferences for specific male phenotypic traits, including bright body colouration and large body size (Godin & Dugatkin 1995, 1996; Dugatkin 1996b; Houde 1997; Dugatkin & Godin 1998b). However, under natural conditions, guppies live together in mixed-sex shoals within social networks (Croft et al. 2004), wherein they are likely to receive social information often from nearby conspecifics. One might therefore expect socially-mediated behaviour, such as mate-choice copying, to occur among wild guppies. It is known that, irrespective of inherent mate preferences, female guppies will reverse their initial mate preference when exposed to social cues from previously observed sexual interactions between other females and particular males (e.g. Dugatkin & Godin 1992; Godin et al. 2005). Under relatively high local densities (as occurs in the Quaré River), social interactions and social information transfer between individuals are common; such conditions would likely promote mate-choice copying as an alternative mate-choice strategy.

One notable difference between my protocol and the one developed by Witte and Ryan (2002) is that I used a pseudo-model female to control for differential activity of the paired stimulus fish, whereas they did not. In this way, it could be argued that my protocol provided a more rigorous test of mate-choice copying in wild fish; however, despite their acknowledgement of the possibility that stimulus fish activity may have differed, Witte & Ryan were confident that the possible effects of this were negligible. In the current study, the pseudo-model female was always kept hidden from subject females swimming in the corridor between the tanks; however, a possibility exists that subject females entering the corridor from a particular angle may have briefly sighted the pseudo-model upon approaching the stimulus fish. Although this may have altered

subject female behaviour, I feel this is unlikely because most females entering the corridor made a fairly rapid decision as to which male they would preferentially visit. This preference decision was probably based on the subject female's observation that one of the stimulus males was always associated with a nearby (model) female and the other stimulus male was not (i.e. viewed as being alone).

Although unlikely, it is possible that we sampled subject females more than once (i.e. pseudoreplication). Pseudoreplication was minimized by testing pools in sequence of their location through progressively moving from downstream to upstream sites, and by conducting trials at sites within discrete pools. After being used in trials, all subject and model fish were released into their testing pools and new individuals replaced them at other sites. The pools were selected to be sufficiently spaced apart (within sites, mean \pm SE inter-pool distance = 46.2 ± 8.0 m) such that repeated sampling of the same subject females was unlikely to occur. Within a pool, paired *Experimental* and *Control Treatments* were separated by a minimum of 2 hrs, one being conducted in the morning and the other in the afternoon.

Although the results reported here are consistent with mate-choice copying behaviour, they do not directly demonstrate mate copying by individually-identified guppies in the wild. This is owing to the difficulties inherent in quantifying the behaviour of unmarked, free-ranging fish and to the particular protocol used in my study. Rather than quantifying the behaviour of known individuals, this protocol quantifies the collective behaviour of several females at a particular location in the river over a defined period of time. While it may have been preferable to have used the rigorous mate-reversal protocol developed by Dugatkin & Godin (1992), this was neither practical nor feasible

in the field. Nonetheless, the results reported here are collectively consistent with mate-choice copying behaviour, and strongly suggest that female guppies in the wild (at least in the Quaré River) pay attention to the mating activities of other nearby females, and use this social information in their mate-choice decisions.

The current field study provides strong evidence for the expression of mate-choice copying behaviour in one natural guppy population (Quaré River). This work is preliminary however. Additional studies on wild populations are necessary to further elucidate the prevalence and generality of mate-choice copying in nature, the factors and conditions that favour such behaviour, and the benefits accrued to females who copy rather than choose mates independently. The fact that female guppies will mate-choice copy both in the laboratory (refs. loc. cited) and in the wild (this study) suggests that this behaviour is not an artefact, but rather that it may be an alternative mate-choice strategy in this species.

CHAPTER 3

THE ROLE OF FAMILIARITY IN MATE-CHOICE COPYING

3.1. INTRODUCTION

There is substantial evidence indicating that female Trinidadian guppies will copy the observed mate choice of other female conspecifics under certain circumstances in the laboratory (e.g. Dugatkin 1992; Dugatkin & Godin 1992; Gibson & Höglund 1992), and female guppies appear to mate-choice copy in the wild (see Chapter 2). This decision by 'observer' females to copy other 'demonstrator' females may be the result of the observer female's inability to independently search for, assess, and select among males due to the various costs associated with these tasks (see Chapter 1 for review). Instead, females may use alternative mate-choice strategies when faced with this challenge (Wade & Pruett-Jones 1990; Pruett-Jones 1992; Gibson & Höglund 1992; Dugatkin 1998; Westneat et al. 2000).

As discussed more extensively in Chapter 1, mate-choice copying is a rudimentary form of cultural transmission whereby information about potential mates is spread among individuals through social interactions (Boyd & Richerson 1985; Dugatkin 2000). While copying behaviour has been investigated extensively in the laboratory, the social mechanisms underlying this behaviour are only moderately understood. Without doubt, many forces shape the manner in which socially-conveyed information about potential mates is expressed by a signaler and further understood and used by a receiver. In this context, the associations that are established between signaling and receiving individuals may influence the prevalence of mate-choice copying behaviour.

The principal aim of my investigation was to test whether the social relationship between ‘communicating’ individuals has an influence on the degree to which mate-choice copying behaviour is expressed. Specifically, I tested whether the social association (i.e. degree of familiarity) between an observer (‘focal’) and a demonstrator (‘model’) female influences the observer female’s tendency to mate-choice copy. I manipulated the social ‘status’ of the model female, as being either a ‘familiar’ or ‘unfamiliar’ individual to the observer female, and predicted that an observer female would be more likely to, and would more strongly, copy a familiar model female than an unfamiliar model female. This expectation was based on a priori theory that individuals are more likely to trust and use social information provided by familiar individuals than unfamiliar ones in their own decision making (Swaney et al. 2001; Griffiths 2003; Ward & Hart 2003). In nature, guppies are known to form social networks, wherein social associations between individual females occur and remain stable over several days (Croft et al. 2004). Such associations are likely to favour the development of social familiarity between individuals.

3.2 MATERIALS AND METHODS

3.2-1. *Experimental Species*

I selected the guppy as my study species (see Chapter 1), as it is a highly promiscuous poeciliid fish, lives in mixed-sex shoals wherein there are opportunities to form social associations and observe other matings (Houde 1997; Magurran 2005), and is known to mate-choice copy when given the opportunity to do so (e.g. Dugatkin 1992; Dugatkin & Godin 1992; Chapter 2). Guppies used in this study were all sexually mature,

first generation (F_1) descendants, bred and reared under laboratory conditions from a stock population of wild adults originally collected from the Quaré River, Trinidad, West Indies ($10^{\circ}41'25''\text{N}$, $61^{\circ}11'51''\text{W}$) in April 2007. Wild-caught fish and their F_1 descendants were housed in aquaria containing a cream-coloured gravel substratum and filtered, aged tap water maintained at 24 - 26°C, and kept under a 13hL/11hD cycle. The fish were fed ad libitum 2-3 times daily with NutraFin flake food, supplemented approximately once daily with *Artemia* sp. (brine shrimp nauplii).

Wild-caught guppies were bred in a large communal tank (120 cm x 45 cm x 50 cm; L x W x H; 284 L) and newly-born offspring were removed and isolated into 10 smaller holding aquaria (40 cm x 20 cm x 25 cm; L x W x H; 16 L). I separated individuals into groups to establish a number of separate pools of either 'familiar' (known conspecifics within a shared tank) or 'unfamiliar' (unknown conspecifics raised in a separate tank) individuals. Opaque partitions separated holding tanks, such that fish within a tank were unable to view or interact with 'unfamiliar' in adjacent tanks. Recognition based on familiarity in guppies takes at least 12 days to develop (Griffiths & Magurran 1997). As test females were raised together in groups of approximately 5-10 individuals for several months, I was confident that familiarity had been established between them and they would later be able to recognize one another in experimental trials. Although possible, it is unlikely that unfamiliar kin would later recognize one another, because guppies distinguish kin via familiarity and kinship has little effect on guppy preferences for familiar individuals (Griffiths & Magurran 1999).

As soon as males developed a gonopodium (male sexual organ) and body colour, they were removed from these tanks and placed in a separate holding tank for later use as

stimulus individuals. Physical isolation of males and females was necessary to ensure that experimental females were virgins and sexually receptive at maturity when tested later for their mate choice (Luyten & Liley 1991; Houde 1997; Magurran 2005). Although kept isolated from male chemical cues, females were visually exposed to males (held in separate adjacent containers) several times weekly to ensure they had some experience with male courtship prior to testing.

Over several months of breeding and rearing fish, I was able to raise a sufficient number of fish to conduct both Experiment 1, wherein I tested for mate-choice copying among familiar and unfamiliar individuals, and Experiment 2, wherein I tested for mate-choice copying when the difference in body colouration between stimulus males was increased (see below).

3.2-2. General Protocol

All experiments were conducted in the same apparatus, which consisted of a test aquarium (60 cm x 31 cm x 31 cm; L x W x H), divided into five sections. Two equally-sized end compartments were separated from the larger central compartment by perforated clear plastic partitions. Lines drawn along the outside of the tank delineated two mate-preference zones, each spaced at 7.5 cm on the interior side of the plastic partitions (Fig. 3-1). A brown corrugated plastic sheet was secured along the two inner tank walls of the central section to reduce reflections. Brown cardboard, spaced approximately 2 cm away from the tank walls, surrounded the tank exterior to provide a uniform background and to reduce external disturbances. A layer of cream-coloured gravel covered the bottom of the tank. The tank was illuminated overhead with Sun Glo

fluorescent tubes, which simulate the spectrum of sunlight. Water (24- 26°C) was replaced between treatments (and prior to new focal female being introduced into the tank) to eliminate any residual chemical cues.

In all mate-choice trials, the fish were videotaped using a SONY (HDR-HC7) digital camera recorder mounted approximately 65 cm above the experimental apparatus. A trial consisted of two consecutive 10-min mate preference tests (described in detail below). Prior to the start of each trial, four clear rectangular Plexiglas canisters were filled with water and placed adjacently in pairs, two situated in either end compartment of the tank (Fig. 3-1). One end canister (the one that would contain the model female) was perforated to allow water exchange between itself and the central compartment of the tank, whereas the other end canisters (the two that would contain stimulus fish and the one that would contain the pseudo-model female) were of non-perforated Plexiglas. Canisters could be easily manipulated and moved as necessary throughout trials. This apparatus design permitted the focal female to visually observe both stimulus fish (in preference tests 1 and 2), and to both visually and chemically sense the model female adjacent to one of the stimulus fish (in preference test 2).

Two binary mate-choice experiments, involving a total of 5 separate *Treatments*, were carried out. Experiment 1 comprised 1) an *Experimental Treatment*, which tested for consistency in female preference for a male (*Treatment A*) and for mate-choice copying behaviour when model females were either familiars (*Treatment B*) of non-familiars (*Treatment C*) using paired males (closely matched for phenotypic traits) as stimulus fish, and 2) a *Control Treatment*, which tested for shoaling behaviour by removing the sexual context and replacing the paired stimulus males with stimulus

females. Experiment 2 comprised a second *Experimental Treatment*, which tested for mate-choice copying behaviour when model females were familiars (*Treatment B*), but using paired stimulus males that were more different phenotypically (compared with those used in *Treatment B* of Experiment 1).

Before beginning a trial, both stimulus males (used in *Experimental Treatments*) and stimulus females (used in the *Control Treatment*) were paired and closely matched for body length. As it is known that female guppies generally have inherent preferences for larger and more brightly coloured males (Endler & Houde 1995; Godin & Dugatkin 1995, 1996; Dugatkin 1996b; Houde 1997; Dugatkin & Godin 1998b), paired stimulus males were also closely matched for body colour. This close matching was performed to eliminate any preceding biases stemming from inherent female preference functions for these male traits. To facilitate male pairings, males were initially given an identification number, measured for total body length (mm) on a measuring board, and their left lateral-side silhouette, including orange and black spots, drawn on paper to facilitate individual identity. During pairings, colour matching was initially performed visually to minimize stress that may arise from handling fish prior to photographing them. At the end of a behavioural trial, each numbered male was placed in a small Plexiglas tube immersed in a water-filled container and photographed (on the left lateral side) with a digital camera. The total body colour area (black and orange) of each male was later quantified using *Image J* computer software. Post-hoc *paired t-tests* were used to compare the mean body lengths and body colour area measurements of paired stimulus males for each of the *Experimental Treatments* separately, and to compare the mean body lengths of paired stimulus females in the *Control Treatment*.

Although adult female guppies tend to be larger than males (Houde 1997), they cannot be distinguished from one another by body colour alone as they are uniformly grey in colour. However, depending on differences in female body size, males may choose to interact with and court females to varying degrees (Herdman et al. 2004). Introduced model and pseudo-model females were therefore paired and matched according to body lengths (to differ by less than 1 mm) to control for this possibility and to increase the likelihood that stimulus males would court both females equally. Both model and pseudo-model females were also of either equal or larger size to focal females, as females will copy the mate choice of larger (older and likely more experienced) females but not of smaller (younger and likely naïve) females (Dugatkin & Godin 1993).

I assessed mate-choice copying using the ‘mate-preference reversal’ protocol designed and used by Dugatkin (1992) and Dugatkin & Godin (1992) in their initial work on female mate-copying behaviour. They defined mate-choice copying as the reversal of an initial female preference for a given male to a previously non-preferred male who was recently observed sexually interacting with a model female. For a given trial, each stimulus fish (stimulus male in the *Experimental Treatments*, and stimulus female in the *Control Treatment*) from a matched pair was initially placed in diagonally-opposite compartments of the test tank (Fig. 3-1). A focal female was placed in a clear, perforated Plexiglas cylinder in the centre of the apparatus. Once fish were introduced into the apparatus, the focal female was given an initial 20-min acclimation period in her central cylinder, followed by the removal of opaque partitions in front of the end compartments (initially blocking her view of the stimulus fish) and a 10-min viewing period, during which she could observe the stimulus fish. Following this viewing period, the opaque

partitions were replaced for 5 min and then removed again for preference test 1. The central cylinder was gently raised out of the tank, releasing the focal female to swim freely for the first 10-min preference test. During this period, I recorded the amount of time the focal female spent near (within the preference zone, i.e. < 7.5 cm) and facing ($0 \pm 90^\circ$) either stimulus fish, two criteria previously established as indicators of female mate choice (Dugatkin & Godin 1992, 1993, 1998a).

After this initial 10-min preference test, the focal female was returned to her central cylinder, the opaque partitions were replaced, and she was left to acclimate for another 20-min period. For *Treatment A*, this protocol was repeated identically for preference test 2. For *Treatments B* and *C*, however, during the second acclimation period a model female was placed in the (perforated) compartment adjacently to the initially 'non-preferred' stimulus fish from preference test 1. Similarly, a pseudo-model female was placed in the (unperforated) compartment adjacent to the initially 'preferred' stimulus fish, but was kept hidden from view by an opaque partition covering the front of its canister (Fig. 3-1). The pseudo-model female was used to control for potential differential activity of the stimulus fish (Schlupp et al. 2004). Following this acclimation period, the large opaque partitions were removed, and the focal female was given another 10-min viewing period wherein she could now observe the initially 'non-preferred' stimulus fish interact with the model female. The opaque partitions were then replaced for 5 min, and the model and pseudo-model females were discretely removed from their end compartments. For preference test 2, the opaque partitions were again removed, and the central cylinder was gently raised to release the focal female and allow her to freely associate with either stimulus fish. As for the first preference test, the time spent by the

focal female near (in the preference zone) and facing either stimulus fish was recorded.

‘Preference’ was defined as a focal female having spent more than 55% of her time near and facing a particular stimulus fish; this association time has been shown to correlate well with a female’s choice of mate when actual mating is allowed (Bischoff et al. 1985; Dugatkin & Godin 1992).

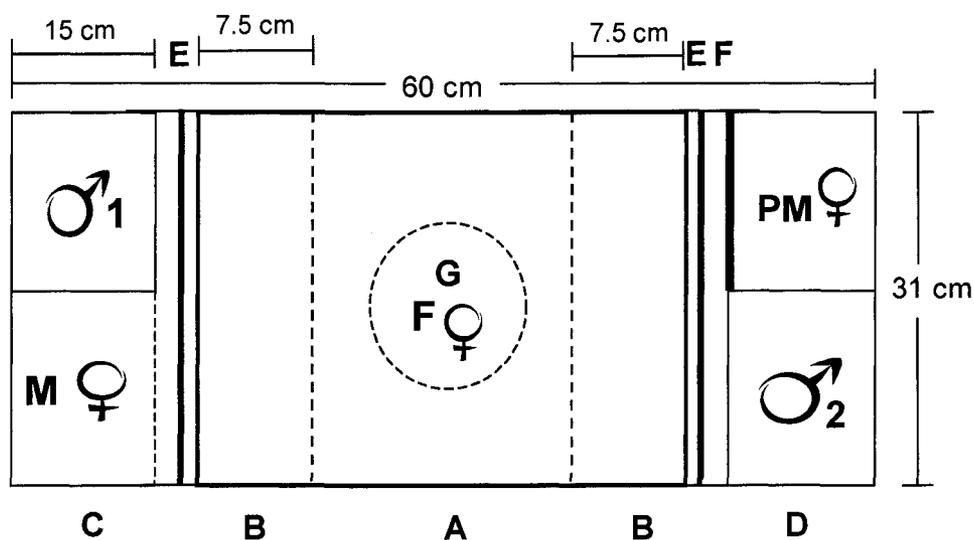


Figure 3-1: Overhead view of the experimental apparatus. The test aquarium was partitioned into 5 sections: A) Central section with perforated Plexiglas cylinder (G) holding the Focal female (F-female); B) Mate-preference zones; C) End compartment containing Male 1 and Model female (M-female); D) End compartment containing Male 2 and Pseudo-model female (PM-female), blocked by opaque partition (F). Removable opaque partitions (E) separate the central compartment from the end compartments.

3.2-3. Experiment 1: *Mate-choice copying when males are phenotypically similar*

Experiment 1 involved two principal components: *Experimental Treatments*, which tested for female preference and mate-choice copying behaviour when paired stimulus males are closely matched phenotypically, and a *Control Treatment*, which tested for shoaling behaviour by replacing stimulus males with stimulus females. Both *Experimental* and *Control Treatments* use the same 'General Protocol' as described above (see section 3.2-2), but each with minor variations. There were three *Experimental Treatments*: *Treatment A* tested for consistency in female preference for a particular stimulus male, *Treatment B* tested for mate-choice copying behaviour using familiar females as models, and *Treatment C* tested for mate-choice copying using non-familiar females as models. All three *Experimental Treatments* used paired males that were closely matched for body length and colour (< 1% difference) as stimulus fish. When testing for mate-choice copying behaviour in *Treatments B* and *C*, females were introduced as models (and hidden pseudo-models) to be visually associated with stimulus males. The *Control Treatment* tested for shoaling behaviour by removing the sexual context (stimulus males replaced by paired stimulus females).

Previous work has shown that female guppies will mate-choice copy when males differ minimally (between 12 and 24%) in orange body colour; however, when their colour differs by more than 40%, females will instead choose the brighter of two males (Dugatkin 1996b). I therefore attempted to closely match males for phenotypic traits, to minimize body length and colour differences between pairings. Within any given trial, wild males were consistently matched with wild males, while F₁ generation males were

matched with other F_1 males. This was done to keep body size pairings consistent and to avoid any potentially confounding variables.

3.2-3. A) *Experimental Treatments*

In a repeated-measures design, each focal (test) female ($N= 36$) was used in three different randomly-ordered treatments (*Treatments A, B, and C*), which were run over three consecutive days (one treatment per day). Following the *Experimental Treatments*, focal, model, and pseudo-model females were returned to their respective isolated tanks to keep social associations distinct, and were used again later in the *Control Treatment*. Only after females had been used once as focal individuals, could they be used again as models or pseudo-models.

Treatment A- No copying opportunity

This treatment tested for consistency in the initial mating preference of focal females. Trials comprised two consecutive choice tests (see 3.2-2. General Protocol), wherein there was no copying opportunity (no model present). The first preference test aimed to determine the initial preference of the focal female for a particular male from a pair of stimulus males, and the second preference test intended to confirm whether her initial mate preference remained consistent. For each trial, the paired stimulus males were similar in total body length (mean \pm SE, male 1 = 23.0 ± 0.4 mm; male 2 = 22.8 ± 0.4 mm; *paired t-test*, $t= 2.04$, $P= 0.14$, $N= 32$, two-tailed; Appendix Fig. 1a) and in percent total body colour (black and orange) area (male 1 = $9.9 \pm 0.04\%$; male 2 = $9.8 \pm 0.06\%$; *paired t-test*, $t= 2.04$, $P= 0.94$, two-tailed; Appendix Fig. 1b).

Treatment B- Familiar model females

Treatment B tested whether females would reverse their initial preference for a particular stimulus male in preference test 1 for the other stimulus male, which she had previously observed consorting with a familiar model female, in preference test 2. The same ‘General Protocol’ (section 3.2-2) was carried out. However, for the second viewing period, a familiar model female was introduced adjacently to the initially non-preferred male, and a paired pseudo-model female (kept hidden from view by an opaque partition) was introduced adjacently to the initially preferred male.

On average, body length varied significantly between focal, model, and pseudo-model females (*One-way ANOVA*: $F=11.93$, $df= 2,105$, $P<0.001$; Fig. 3-2); however, this variation was attributable to body size differences between focal and model females, and between focal and pseudo-model females, but not between paired model and pseudo-model females (*Tukey’s multiple comparison test*: $P= 1$; Fig. 3-2). These results confirm that model and pseudo-model females were successfully paired and appropriately size matched with focal females.

Again for each trial, the paired stimulus males were similar in total body length (mean \pm SE, male 1 = 23.0 ± 0.3 mm; male 2 = 22.9 ± 0.3 mm; *paired t-test*, $t= 2.03$, $P= 0.82$, $N= 36$, two tailed; Appendix Fig. 1a) and percent total body colour (black and orange) area (male 1 = $10.0 \pm 0.04\%$; male 2 = $10.0 \pm 0.05\%$; *paired t-test*, $t= 2.03$, $P= 0.89$, two-tailed; Appendix Fig. 1b).

Treatment C- Unfamiliar model females

Treatment C tested whether females would reverse their initial preference for a particular stimulus male in preference test 1 to prefer the other stimulus male, which she had previously observed consorting with an unfamiliar model female, in preference test 2. This protocol was identical to that of *Treatment B*, except that model females introduced in preference test 2 were now unfamiliar individuals to the focal females.

Paired model and pseudo-model females in each trial were size matched to be similar to one another in body length, and equal or larger in body length to the focal female. As intended, the body length difference in pairings was only evident between focal and model females, and between focal and pseudo-model females, but not between model and pseudo-model females (*One-way ANOVA: F= 30.85, df= 2,105, P<0.001; Tukey's multiple comparison test: P= 0.201; Fig. 3-2*).

Paired stimulus males were similar in their mean (\pm SE) body lengths (male 1 = 23.0 ± 0.3 mm; male 2 = 23.3 ± 0.3 mm; *paired t-test, t= 2.03, P= 0.15, N= 36, two tailed; Appendix Fig. 1a*) and percent total body colour (black and orange) area (male 1 = $9.5 \pm 0.04\%$; male 2 = $9.0 \pm 0.04\%$; *paired t-test, t= 2.03, P= 0.20, two-tailed; Appendix Fig. 1b*).

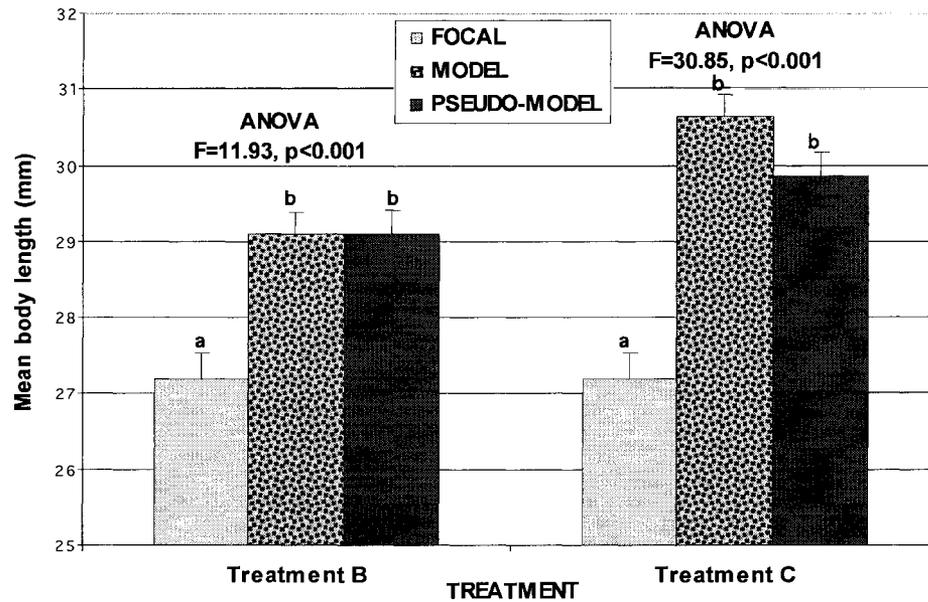


Figure 3-2: Mean (+ SE) total body length (mm) of focal, model, and pseudo-model females used in both *Treatments B* and *C*. Body lengths are compared within each treatment separately using the *ANOVA*. Means with similar letters above them are not statistically different from each other ($P > 0.05$), whereas means with dissimilar letters are significantly different ($P < 0.05$) from each other.

3.2-3. B) *Control Treatment: Control for shoaling behaviour*

The *Control Treatment* was carried out to ascertain whether the behaviour of the focal females observed in *Treatments B* and *C* of the *Experimental Treatment* was sexually motivated and not simply the result of shoaling with other individuals. This protocol was identical to that used in *Experimental Treatment B* (wherein model females were familiar to the focal females), except for one critical difference: the sexual context was removed by replacing the paired stimulus males with paired stimulus females. I ran 24 replicates of the *Control Treatment*, wherein I expected random focal female preference for either stimulus female rather than female choice reversals between preference tests. Random choice would indicate that females were not shoaling with other individuals, and would thereby suggest that any preference reversals in *Treatments B* and *C* of *Experimental* trials reflect mate-choice copying rather than shoaling behaviour.

Within a given trial, stimulus females were matched for total body length (mean \pm SE, female 1 = 30.7 ± 0.6 mm; female 2 = 30.3 ± 0.5 mm; *paired t-test*, $t = 2.07$, $P = 0.06$, $N = 24$, two-tailed; Appendix Fig. 2). Paired model (30.9 ± 0.4 mm) and pseudo-model (29.7 ± 0.4 mm) females were similar in length, and equal to or larger than focal females (29.9 ± 0.7 mm) (*One-way ANOVA*: $F = 1.46$, $df = 2,69$, $P = 0.24$; Appendix Fig. 2).

3.2-4. Experiment 2: *Mate-choice copying when males are phenotypically different*

In Experiment 1, our results did not show consistency in female preference for any particular male across the two preference tests (*Treatment A*), nor did they reveal that females mate-choice copied either familiar (*Treatment B*) or unfamiliar (*Treatment C*) model females. Although female guppies have been shown to mate-choice copy when

stimulus males differ between 12 and 24% (but not by 40%) in orange body colour (Dugatkin 1996b), it is uncertain whether they will mate-choice copy when males are extremely similar in phenotype. I postulated that the results obtained in Experiment 1 could be attributed to an inability of test females to cognitively differentiate between paired stimulus males that are very similar in body size and overall colouration (paired males differed by <1% for both these traits), which may have in turn constrained their ability to mate-choice copy. Here, I wished to ascertain whether this was in fact the case by repeating the protocol of Experiment 1 with paired stimulus males that differed more substantially in body colouration.

In Experiment 2, I tested for mate-choice copying behaviour among familiar individuals (as per Experiment 1, *Experimental Treatment B*), but when the difference in body colouration between paired stimulus males was greater than that in Experiment 1. Owing to the limited number of males available, I was only able to pair stimulus males to differ maximally in total body colour (black and orange) area by 8%, which was still not sufficient to be statistically different on average (male 1 = $11.0 \pm 0.9\%$; male 2 = $9.0 \pm 0.1\%$; *paired t-test*, $t = 2.06$, $P = 0.30$, two-tailed; Appendix Fig. 3). As intended, the paired males were similar in body length (male 1 = 23.7 ± 0.3 mm; male 2 = 23.5 ± 0.3 mm; *paired t-test*, $t = 2.06$, $P = 0.66$, $N = 26$, two-tailed).

Familiar model and pseudo-model females were also matched for body length, such that model (31.7 ± 0.4 mm) and pseudo-model (31.3 ± 0.5 mm) females were similar, and equal to or larger than focal females (28.7 ± 0.4 mm) (*One-way ANOVA*: $F = 14.47$, $df = 2,75$, $P < 0.001$; Appendix Fig. 4). As was intended, this difference was evident between the focal and model females and between the focal and pseudo-model

females (*Tukey's multiple comparison test*: $P=0$, $P=0$, respectively), but not between the model and pseudo-model females (*Tukey's multiple comparison test*: $P=0.822$).

3.3. RESULTS

3.3-1. Experiment 1: *Mate-choice copying when males are phenotypically similar*

Experimental Treatments

In *Treatment A*, the observed relative number of females (expressed as a percentage value) preferring the more brightly coloured male in both preference test 1 (*G-test with Williams correction*: $G_{adj}=0.123$, $P>0.7$, $N=32$) and preference test 2 ($G_{adj}=1.114$, $P>0.25$, $N=32$) did not differ significantly from chance (i.e. 50%). Similar results were obtained for *Treatment B* (preference test 1: $G_{adj}=0.439$, $P>0.5$, $N=36$; preference test 2: $G_{adj}=1.768$, $P>0.15$, $N=36$), and for *Treatment C* (preference test 1: $G_{adj}=0$, $P=1.0$, $N=36$; preference test 2: $G_{adj}=0.439$, $P>0.5$, $N=36$; Fig. 3-3a). Across all three *Treatments* (Fig. 3-3b), the amount of time focal females spent near the preferred male was similar (2-way ANOVA, Treatment effect: $F=0.604$, $df=2,202$, $P=0.55$). Similarly, there was no variation in fish behaviour between the two preference tests (Test effect: $F=0.92$, $df=1,202$, $P=0.34$) and no significant statistical Treatment x Test interaction ($F=0.16$, $df=2,202$, $P=0.85$).

It can therefore be concluded that focal females were consistent in their choice of mate between the two consecutive preference tests, but did not prefer the more brightly coloured male over the slightly drabber male. This result indicates that females will not necessarily prefer the brighter of two males when they are closely matched phenotypically, regardless of whether males are viewed independently (*Treatment A*) or

interacting with a model female (*Treatments B and C*). This finding is as expected, and based on theory (Gibson & Höglund 1992), provides the conditions favouring mate-choice copying.

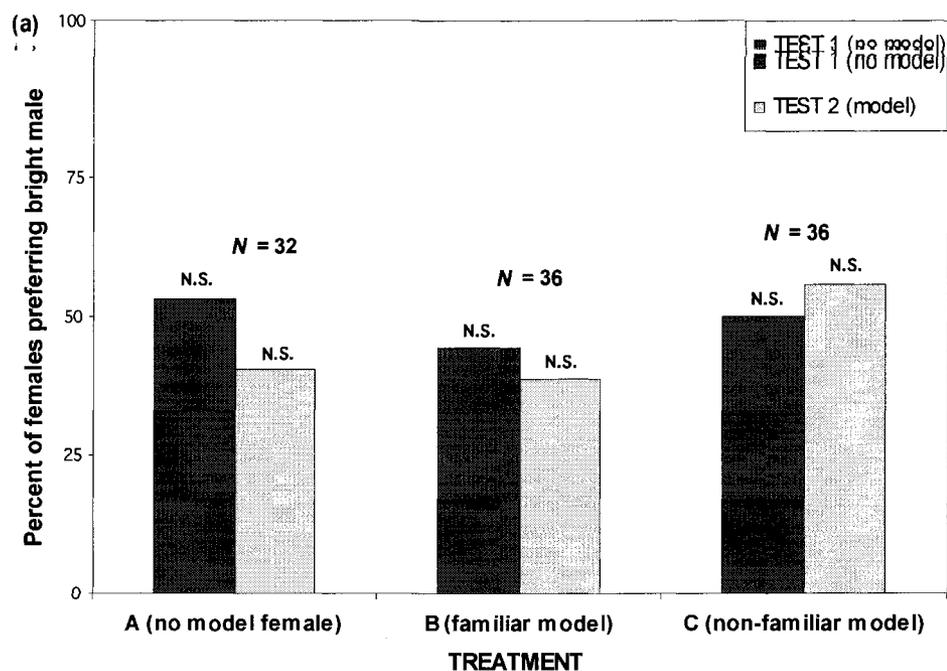


Figure 3-3: (a) Within treatment comparisons (*Treatment A*- no copying opportunity; *Treatment B*- copying opportunity with familiar model female; *Treatment C*- copying opportunity with unfamiliar model female) of the relative number (given as a percentage value) of focal females expressing a preference for the brighter stimulus male in preference tests 1 and 2. ‘N.S.’ denotes non-significant difference between observed value and value expected by chance (50%) for each preference test separately (*G-test* with *Williams correction*). ‘*N*’ denotes the number of focal females tested.

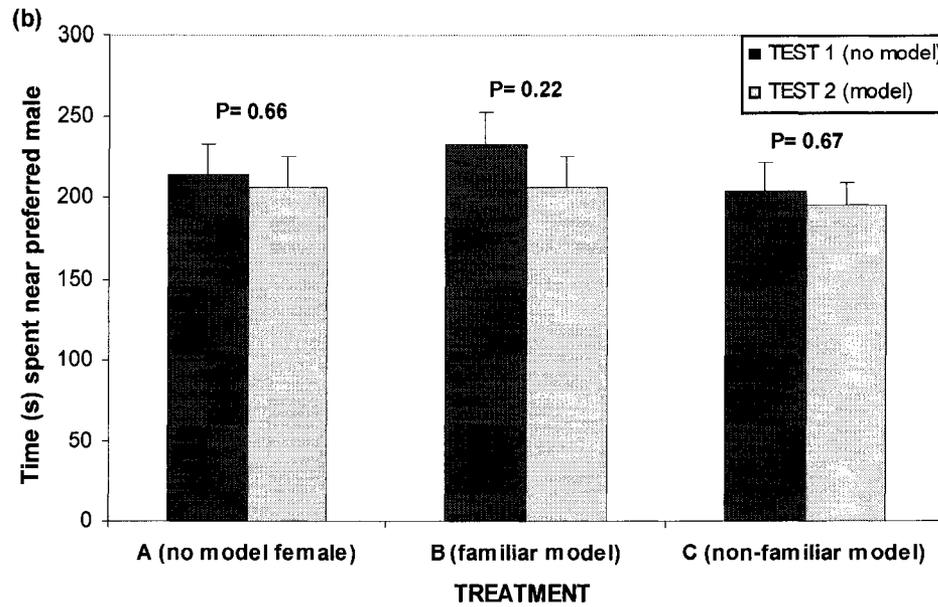


Figure 3-3: (b) Mean + SE time (s) spent by focal female near the preferred male in preference tests 1 and 2, within each Treatment (*Treatment A*- no copying opportunity; *Treatment B*- copying opportunity, familiar model female present; *Treatment C*- copying opportunity, non-familiar model female present. *P-values* shown were obtained using the *paired t-test*.

Overall, on average (\pm SE) focal females spent $45.3 \pm 2.04\%$ of their total test time (i.e. 271.7 ± 12.2 s out of 600 s) near and facing both paired stimulus males (i.e. in both preference zones) compared to that expected by chance (i.e. 25% of their time, or 150 s) if they were swimming about randomly throughout the tank (see Appendix Fig. 5 for percent preference time comparisons within and across *Treatments*). The focal females were thus choosing to spend considerable time near and interacting with courting stimulus males, suggesting that they were sexually motivated and not simply swimming randomly about the tank. Within *Treatment* comparisons suggest that focal females were spending slightly more of their total test time in stimulus male preference zones during preference test 1 than during preference test 2; this difference was only significant in *Treatment B*, however (*paired t-test*: $P=0.01$, $t=2.03$, $df=35$; Appendix Fig. 5). There was no significant difference in the mean total percent time spent by focal females in male preference zones across the three *Treatments* (2-way ANOVA: $F=0.956$, $df=2,2$, $P=0.51$; Appendix Fig. 5), suggesting that the sexual motivation of focal females was similar among *Treatments*.

Finally, I evaluated whether females were consistent in their preference for a particular male between preference tests 1 and 2 within all three *Treatments*. This was carried out by assessing the number of females that reversed their initial preference for a particular stimulus male in test 1 and preferentially selected the other male in test 2. I statistically compared the number of females actually observed reversing their preference to the theoretical probability of reversals expected to occur randomly by chance (i.e. 50%). In *Treatment A*, wherein there was no model female present (and therefore no copying opportunity), 43.8% of females reversed their initial mate preference between

tests, which is not significantly different from that expected by chance (*G-test with William's correction*: $G_{adj}= 0.494$, $P>0.45$, $N= 32$; Fig. 3-4). One would not expect to see significant variation in the frequency of reversals within this *Treatment*, as females should be randomly selecting either of the two stimulus males both in preference tests 1 and 2, given that males were closely matched in phenotype.

The percentage of female mate-preference reversals observed in *Treatment A*, wherein there was no copying opportunity, was then used as a baseline value for the expected number of reversals in *Treatments B* and *C*. In *Treatment B*, wherein there was a familiar model female present in test 2 (and therefore the opportunity for focal females to copy), only 38.8% of females reversed their initial preference for a particular stimulus male between tests; this frequency of reversals is not significantly different from that expected based on the frequency of reversals observed in *Treatment A* in the absence of a model female (*G-test with William's correction*: $G_{adj}= 0.344$, $P> 0.55$, $N= 36$). A similar result (i.e. 50% of focal females reversing their initial preference) was obtained for *Treatment C*, wherein focal females were presented with the opportunity to copy an unfamiliar model female in test 2 (*G-test with William's correction*: $G_{adj}= 0.559$, $P> 0.4$, $N= 36$).

The frequency of mate-choice reversals between tests 1 and 2 did not differ significantly across all three treatments (*G-test with William's correction*: $G_{adj}= 0.872$, $df= 2$, $P> 0.65$; Fig. 3-4). Given these results, I conclude that Quaré River females were not mate-choice copying, as was expected based on previous studies (Briggs et al. 1996; Dugatkin 2007), but were rather choosing between paired stimulus males randomly.

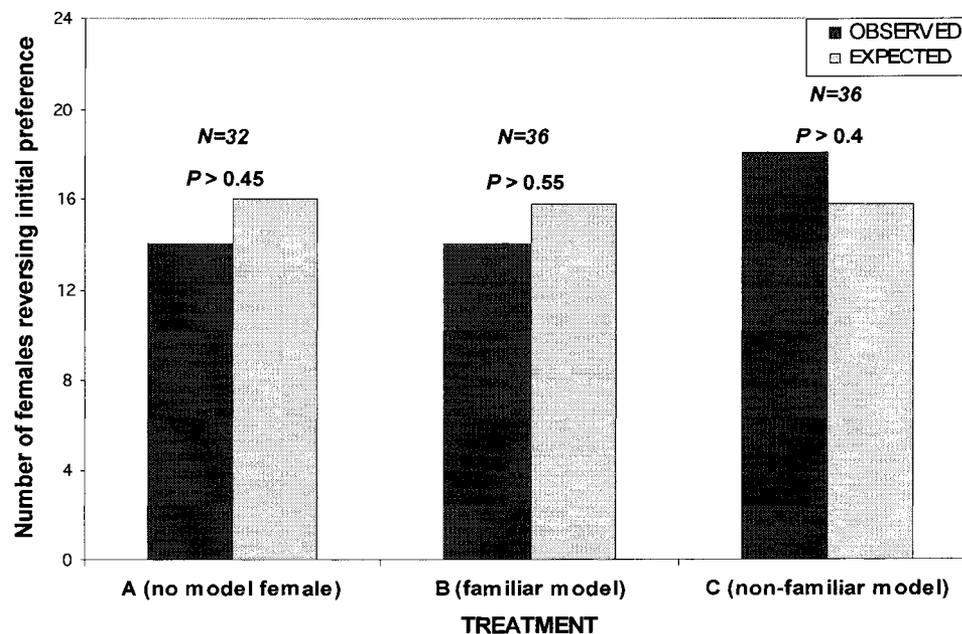


Figure 3-4: Number of females observed reversing their initial preference for a particular stimulus male between preference tests, as compared to the theoretical probability of reversals due to chance (i.e. 50% in *Treatment A*). The percentage of female preference reversals observed in *Treatment A* was used as a baseline for the expected number of reversals in both *Treatments B* and *C*. *P-values* shown were obtained using the *G-test* with *Williams correction*.

Control Treatment

In the *Control Treatment*, the sexual context was removed by replacing the paired stimulus males with paired stimulus females, so as to ascertain whether the behaviour of focal females observed in the *Experimental Treatments* was sexually motivated or simply the result of females shoaling with other individuals. Statistical analyses were performed as in the *Experimental Treatments*, but only within *Treatment* comparisons (i.e. *Treatment B*- copying opportunity with familiar model female present) were made.

To evaluate whether focal females repeatedly preferred a particular stimulus female, their preference for either of the two stimulus females was compared between preference tests 1 and 2. The relative number of females (expressed as a percentage value) preferring to associate with female 1 (arbitrarily selected as the female positioned in the left compartment of the tank) differed marginally between the two preference tests, from that which would be expected by chance (*G*-test with Williams correction: $G_{adj}=3.87$, $P<0.05$, $N=24$); Fig. 3-5a). However, focal females were not consistent across tests in their overall choice of a particular stimulus female. This is reflected in the similar amount of time focal females spent associating ('shoaling') with the 'preferred' stimulus female in preference test 1 (192.0 ± 17.9 s) and test 2 (195.0 ± 22.2 s) (*paired t*-test: $t=2.07$, $P=0.88$, $N=24$; Fig. 3-5b).

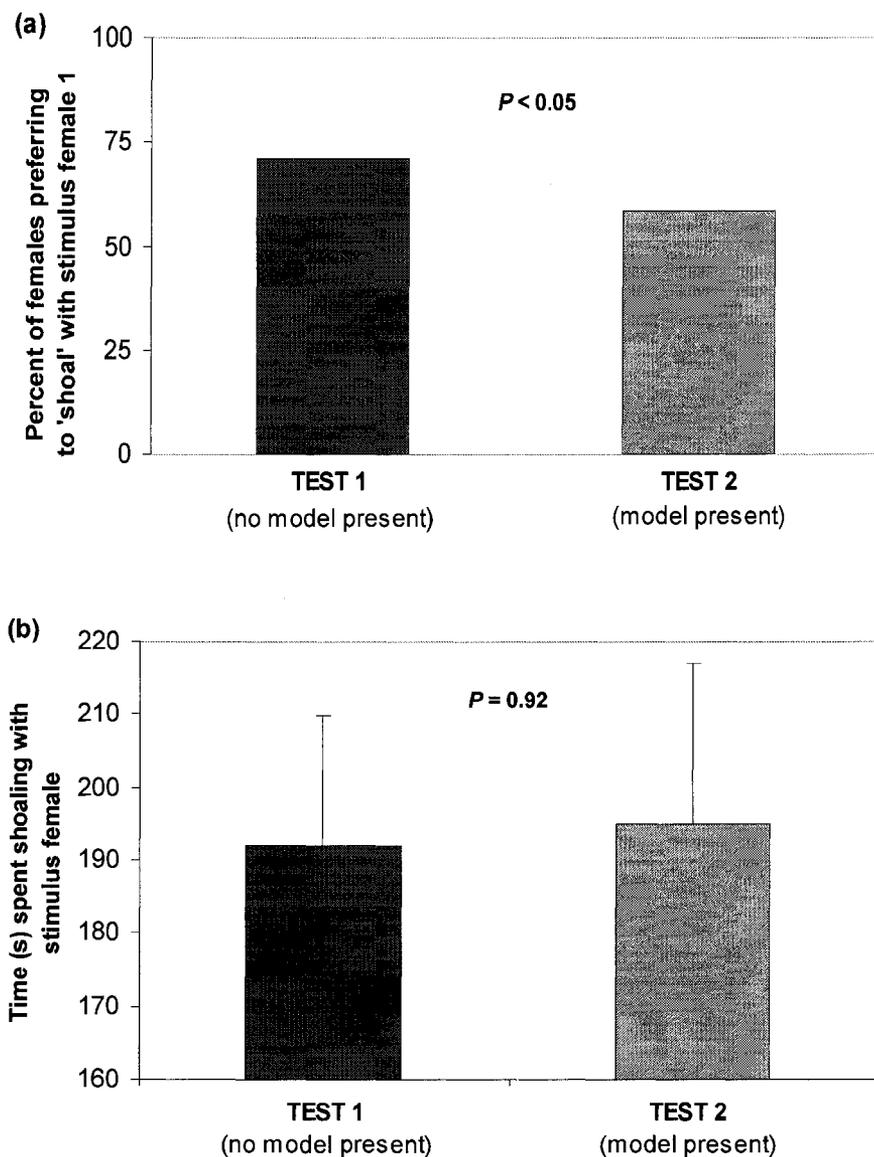


Figure 3-5: (a) Comparison of the relative number (expressed as a percentage value) of focal females preferring stimulus female 1 across preference tests 1 and 2, within the *Control Treatment*. (b) Mean (+ SE) time (s) spent by focal females near the preferred stimulus female in preference tests 1 and 2, within the *Control Treatment*. *P*-values shown were obtained using the *G*-test with *Williams correction* and the *paired t*-test, respectively.

I further evaluated whether focal females were consistent in their choice of a particular stimulus female across preference tests 1 and 2, by assessing the number of females that reversed their initial preference for a given female. Between preference tests, the observed number of female reversals did not differ significantly from that expected by chance ($G_{adj}=0.164$, $df=1$, $P>0.6$, $N=24$; Appendix Fig. 6).

Collectively, these results suggest that focal females did not prefer to socially associate with a conspecific female that they had previously observed near a model female over an apparently lone female, and thus were not shoaling.

3.3-2. Experiment 2: *Increasing the difference in male phenotype*

In Experiment 2, I increased the difference in body colouration between paired stimulus males to ascertain whether mate-choice copying could be promoted by reducing the difficulty that focal females were experiencing in trying to differentiate between males. Data were analyzed in a fashion identical to that of Experiment 1, except that only within-*Treatment* comparisons were made.

Female preference for the more brightly coloured of the two stimulus males was compared between preference tests 1 and 2. The relative number of females (expressed as a percentage value) preferring to associate with the brighter male in the first preference test (57.7%) did not differ significantly from the relative number (69.2%) preferring the brighter male in the second preference test (*G-test with William's correction*: $G_{adj}=1.76$, $P>0.15$, $N=26$; Fig. 3-6a). Moreover, the time focal females spent associating with the 'preferred' stimulus male in preference tests 1 and 2 did not differ (*paired t-test*: $t=2.06$, $P=0.36$, $N=26$). Interestingly, these average preference times (Fig. 3-6b) are

substantially less than those obtained for the three *Experimental Treatments* in Experiment 1 (Fig. 3-3b). Nonetheless, this result suggests that the sexual motivation of focal females did not change across the two tests.

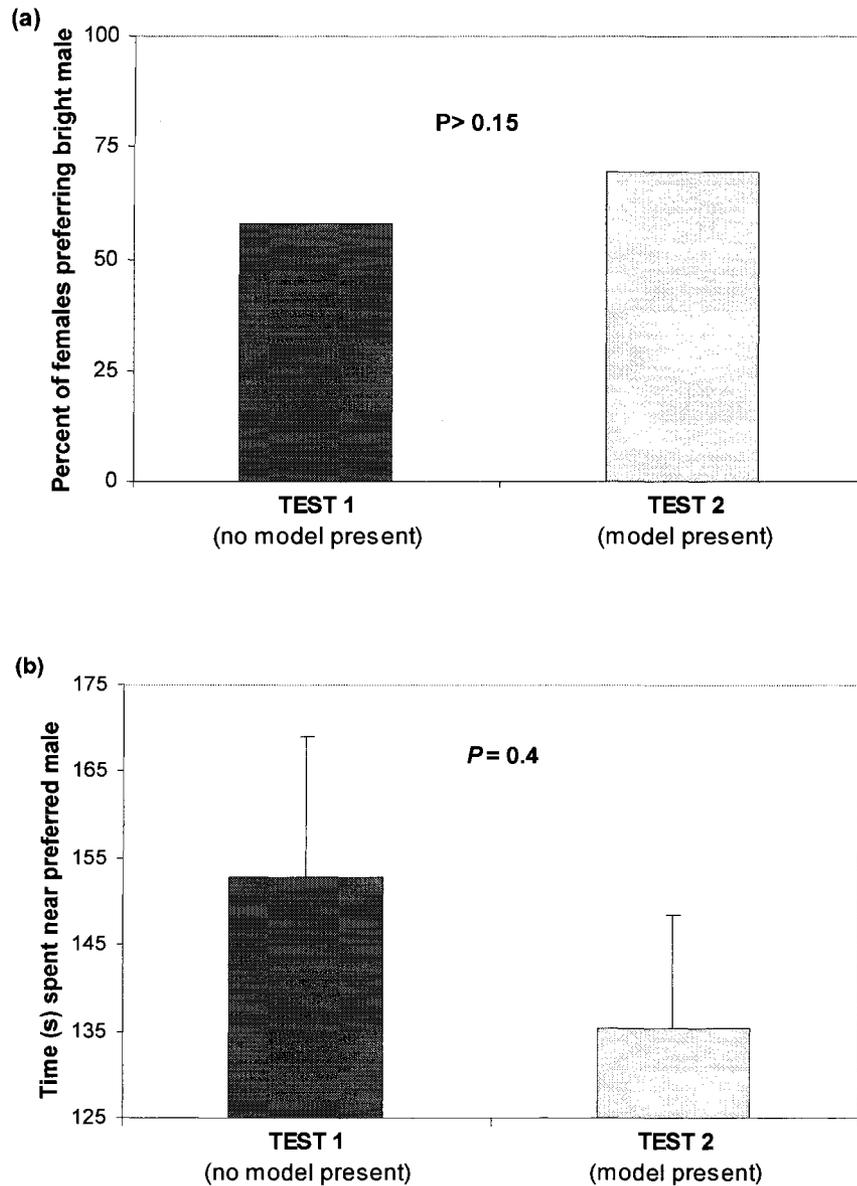


Figure 3-6: (a) Comparison of the relative number (expressed as a percentage value) of focal females preferring the more brightly coloured stimulus male in preference tests 1 and 2, Experiment 2. (b) Mean (+ SE) time (s) spent by focal females near the preferred stimulus male in preference tests 1 and 2, Experiment 2. *P-values* shown were obtained using the *G-test* with *Williams correction* and the *paired t-test*, respectively.

The number of focal females reversing their initial preference for either stimulus male was compared between preference tests 1 and 2. Owing to the presence of a model female near the initially non-preferred male in test 2, female preference reversals would indicate mate-choice copying (cf. Dugatkin & Godin 1992). However, only 42.3% of females reversed their initial preference for a particular stimulus male between the preference tests (Fig. 3-7), a result that does not differ significantly from that expected by chance alone ($G_{adj} = 0.605$, $P > 0.30$, $N = 26$).

Furthermore, I evaluated whether the frequency of female preference reversals exhibited between tests 1 and 2 in *Treatment B* (wherein females were given an opportunity to copy familiar models) differed significantly between Experiment 1 (wherein paired stimulus males were very similar in phenotype) and Experiment 2 (wherein paired stimulus males differed in phenotype). Contrary to expectation, the relative frequency of females reversing their initial preference for a particular stimulus male in Experiment 1 (38.9%) and Experiment 2 (42.3%) did not differ significantly (*G-test with Williams correction*: $G_{adj} = 3.034$, $df = 1$, $P > 0.05$; Fig. 3-8).

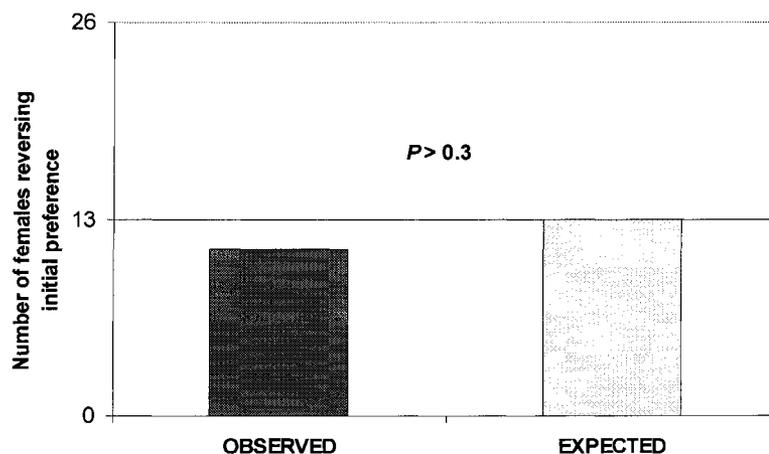


Figure 3-7: Number of focal females observed reversing their initial mate preference between preference tests 1 and 2, as compared to the expected theoretical value based on chance (50%; denoted by the horizontal line). *P*-value was obtained using the *G*-test with *Williams* correction.

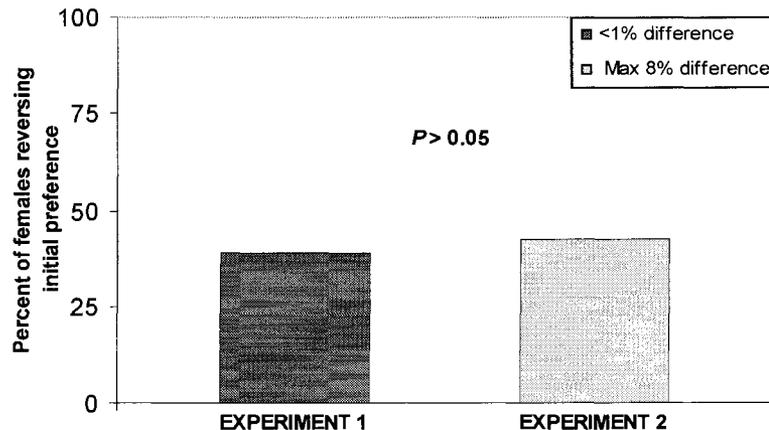


Figure 3-8: Relative number (expressed as a percentage) of focal females reversing their initial preference for a given stimulus male in *Treatment B*, compared across Experiment 1, wherein paired males phenotypically differ by <1%, and Experiment 2, wherein paired males phenotypically differ by a maximum of 8%. *P*-value was obtained using the *G*-test with *Williams* correction.

3.4. DISCUSSION

In Experiment 1, I examined female mating preferences under three different *Treatments* to determine (1) whether females were consistent in their preference for a particular male when given no opportunity to mate-choice copy (*Treatment A*), and (2) whether, when given the opportunity to copy, females would reverse their initial preference for a particular stimulus male and select another male seen associating with a familiar (*Treatment B*) or an unfamiliar (*Treatment C*) model female. In *Treatment A*, females did not exhibit strong choice for either stimulus male and were consistent in their behaviour between the two preference tests (i.e. did not reverse their initial preference). Because the paired stimulus males were very similar in phenotype, and as females were not given an opportunity to copy, it is not surprising that mate choice was random in both preference tests. Focal females appeared to have experienced difficulty in distinguishing between the similarly paired stimulus males and in the absence of a demonstrator (i.e. model) female. When presented with a copying opportunity, females again did not consistently reverse their initial preference for a particular stimulus male between preference tests, either when the male was viewed associating with a familiar (*Treatment B*) or an unfamiliar (*Treatment C*) model female. These results do not provide evidence for mate-choice copying behaviour, nor for any role of familiarity between observer (focal) and demonstrator (model) females on the prevalence of copying in the guppy, under the current laboratory conditions. These findings are unexpected, given that female guppies originating from the Quaré River have been shown previously to mate-choice copy in the laboratory (Briggs et al. 1996; Dugatkin 2007) and in the wild (Chapter 2).

I postulate that the observed lack of consistency in mate-choice copying could be associated with the nature of the stimulus male pairings. Because paired males were so closely matched for body size and colouration (varying by less than 1% in Experiment 1), it is possible that focal females experienced difficulty identifying and differentiating between them. In a second experiment, I attempted to evaluate whether, through slightly increasing the difference in body colour between paired stimulus males, females would be better able to identify individuals and thereby more likely to mate-choice copy. However, despite this adjustment, focal females still did not copy familiar models when given this opportunity.

Although I did not find evidence for mate-choice copying in either *Experimental Treatment B* or *C*, I nonetheless conducted a *Control Treatment* to test for shoaling behaviour. In removing the sexual context by replacing stimulus males with stimulus females, I assessed whether focal females would preferentially associate with a stimulus female observed adjacent to a model female in test 2 (i.e. a shoaling response) or whether they would randomly associate with either stimulus female across preference tests. As focal females spent a similar amount of time on average affiliating with both stimulus females, and did not reverse their initial preference for a particular female to associate with the other focal female between tests, I conclude that choice was random and females were not exhibiting a shoaling response per se. Should consistent mate-choice copying have been observed in the *Experimental Treatments*, this *Control Experiment* result would suggest that the behaviour of focal females exhibited in the *Experimental Treatments* was sexually motivated and not simply the result of shoaling behaviour.

There are several plausible explanations for the observed lack of consistent mate-choice copying behaviour in Quaré River females in the current laboratory study. Initially, I expected that the cognitive challenge of having to discriminate between, and recall the identity of, paired stimulus males that were so closely matched in phenotype, would constrain female mate-copying behaviour. While theory postulates that observer females should more likely mate-choice copy when they cannot independently distinguish between male quality (Gibson & Höglund 1992), they may need to be able to differentiate between males first, at least to a small degree, in order to copy the mate choice of other females. There may be a minimal threshold of phenotypic difference between paired males that must be reached in order for a female to differentiate and choose between two males being compared (see Chapter 4 for further discussion). Above this theoretical threshold, innate preferences for bright colour in males would be expected to primarily determine mate choice in female guppies (Houde 1997), whereas below this threshold individuals would be indistinguishable from one another. Despite my attempts to increase body colour differences between paired stimulus males in Experiment 2, I was only able to pair males to differ in total body colour area by a maximum of 8%, owing to the limited range of phenotypic variation expressed by males in my study sample. Using guppies descended from a population in the Paria River, Trinidad, Dugatkin (1996b) was able to pair stimulus males that differed in their total area of orange colour by up to 40%. He found evidence for female mate-choice copying when males differed in colour by 12% and 24%, but a preference for the brighter male when orange colour differed by 40%. Because my results do not correspond with other studies that provide evidence for mate-choice copying in the guppy (refs. loc. cited), it is possible that stimulus males in

my study were too closely matched in phenotype and that a minimal colour-difference threshold acts to constrain female identification of males in the guppy.

Indiscriminate mate choice and lack of support for mate-choice copying in my laboratory study may also be associated with prior female sexual experience. Naïve guppy females, who have had little previous exposure to males, may initially be more likely to mate arbitrarily (Houde, 1988). Although I provided females with some prior exposure to males, they never had the opportunity to physically interact with males themselves once mature, and were limited to visual cues so that they remained virgins prior to mate preference testing. Although females were able to view males (in an adjacent container) performing sigmoid courtship displays, they never actually observed males naturally interacting, courting, or mating with other females. These pre-test conditions may have constrained the development of natural mating preferences and choice in focal females. As a consequence, focal females, already challenged in identifying males, may have had reduced receptivity to male courtship, and thereby failed to exhibit consistent mate choice and mate-copying behaviour.

Another variable that may have influenced female behaviour is the health of my study population. During fish development in the laboratory, I encountered several bouts of fin rot, a bacterial disease that appears to be endemic in this Quaré River population in Trinidad (personal observation). This infection can spread rapidly among individuals and, if not treated hastily (with antibiotics), can quickly kill fish. During development, most of my F_1 guppies either experienced this condition or were exposed to it via other infected individuals sharing their holding tank. Many individuals were lost as a result; however, those who survived and reached maturity were used in behavioural trials. As this bacterial

condition appears endemic (see Discussion, Chapter 4), there is a possibility that it may have adversely affected the overall health and behaviour of surviving individuals used in my laboratory study. When experimental trials were commenced, most guppies were in good physical condition and appeared to behave in a 'natural' fashion. Although focal females were used only once as test individuals across the three *Treatments* in Experiment 1, they were used again in the *Control Treatment* and in Experiment 2. Stimulus males, as well as model and pseudo-model females, were also used repeatedly throughout the study, because the number of fish available did not allow for single fish use. Repeated use and handling may have also had an adverse effect on overall fish behaviour and on focal female mating decisions, which may explain the unexpected behavioural results observed in the laboratory.

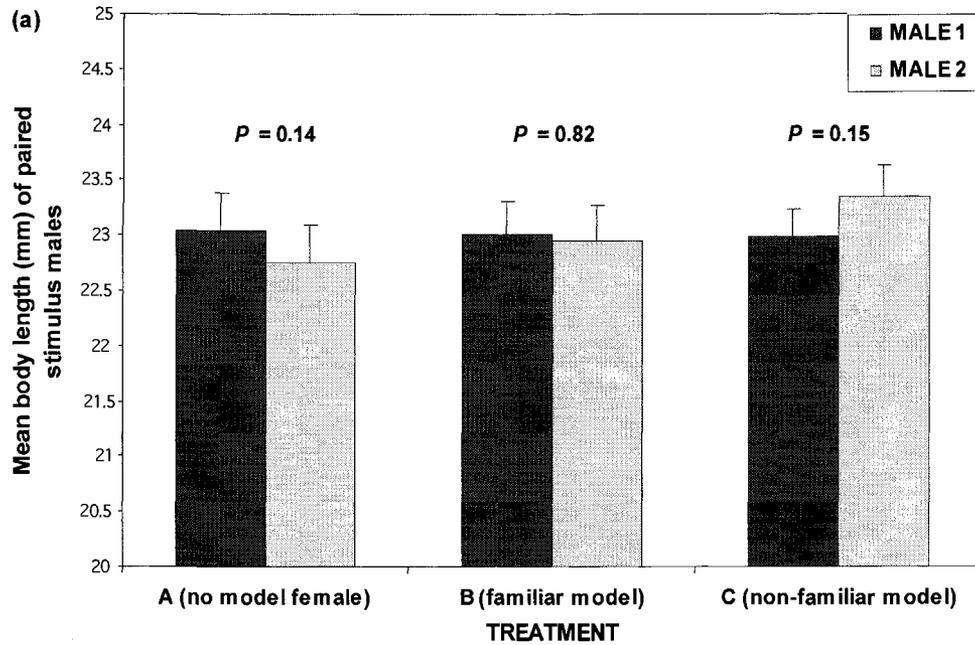
There is substantial evidence for mate-choice copying behaviour in guppies in the laboratory (refs loc. cited; Chapter 2), from studies that employed a protocol very similar to mine here (Dugatkin 1992; Dugatkin & Godin 1992; Briggs et al. 1996). Because certain components of my setup and protocol were very conservative in comparison, however, it is possible that my results are not directly comparable to those of other laboratory studies (refs. loc. cited) that demonstrate mate copying. For example, preference zones in my study were only 7.5 cm in width and preference times were only recorded when focal females were in the section directly in front of the stimulus fish. Other studies (Dugatkin 1992, 1996b; Godin & Dugatkin 1995; Briggs et al. 1996; Dugatkin & Godin 1998a; Applebaum & Cruz 2000; Witte & Noltemeier 2002) have commonly used 10 to 25 cm preference zones, and stimulus fish were generally given the entire end compartment in which to swim, with recorded preference times corresponding

to the zone spanning the entire width of the test tank. Switching the spatial position of stimulus males (between the two consecutive tests), as a control for potential side biases, may also have influenced focal female mate preferences. Although this procedure is commonly used in mate-choice copying studies (e.g. Briggs et al. 1996; Witte & Ryan 1998; Applebaum & Cruz 2000; Witte & Noltemeier 2002; Godin et al. 2005), it may have confused focal females in this laboratory study, particularly as females were relatively inexperienced and stimulus males were closely matched phenotypically.

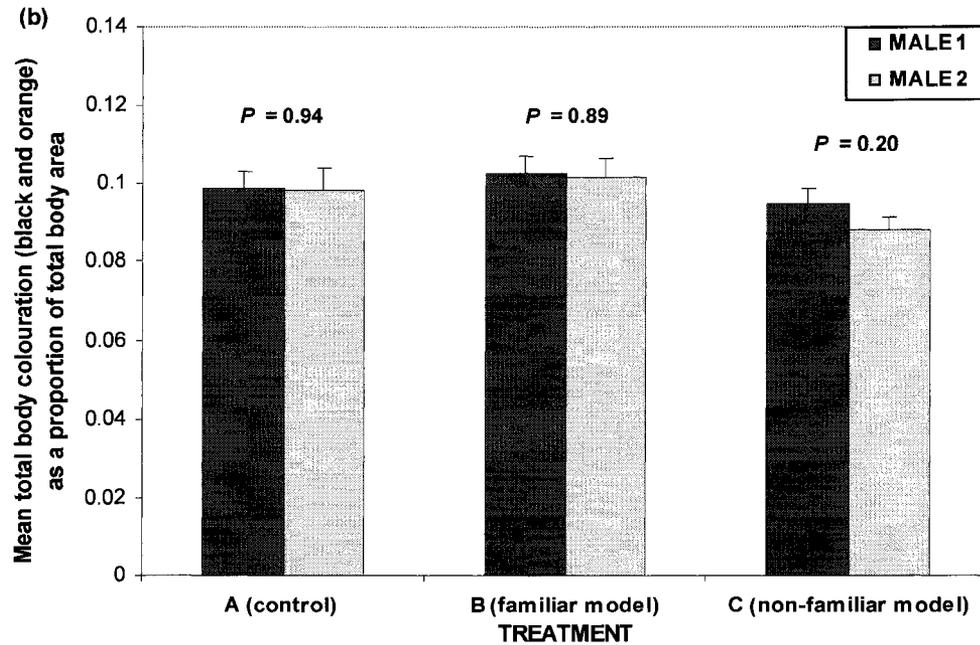
Various other experimental conditions may not correspond to natural conditions that would be experienced by female guppies in the wild. For example, focal females only observed the model female for 10 min, following which the model was removed prior to the second preference test. In nature, females would be more likely to observe a demonstrator female continually interacting with a male, thus receiving continuous social information between the sexually interacting male and demonstrator female. With the artificial removal of this model, a female's tendency to copy might have been reduced.

The current laboratory study investigated the role of social associations between observer and demonstrator females in mate-copying behaviour, and attempted to elucidate the degree to which individuals depend on social information in making mate-choice decisions. Despite the negative results obtained, in theory, social associations are likely to have a strong influence on the use of socially-acquired information in the mating decisions of animals, and therefore are likely to influence the expression and the prevalence of mate-choice copying behaviour. Further research on this topic may help predict the extent to which female guppies form social aggregations in nature and their reliance on social information in decision-making processes.

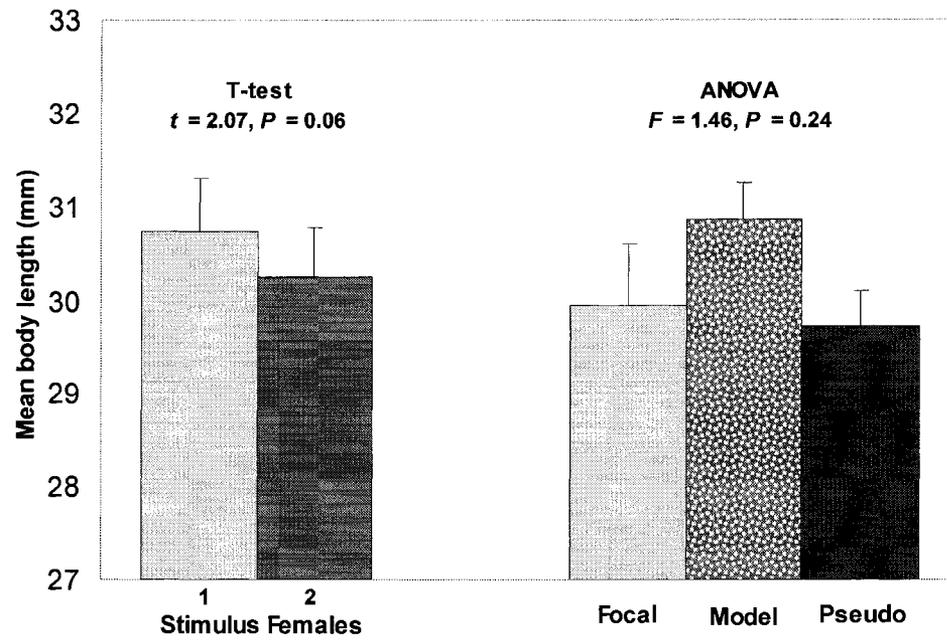
APPENDIX



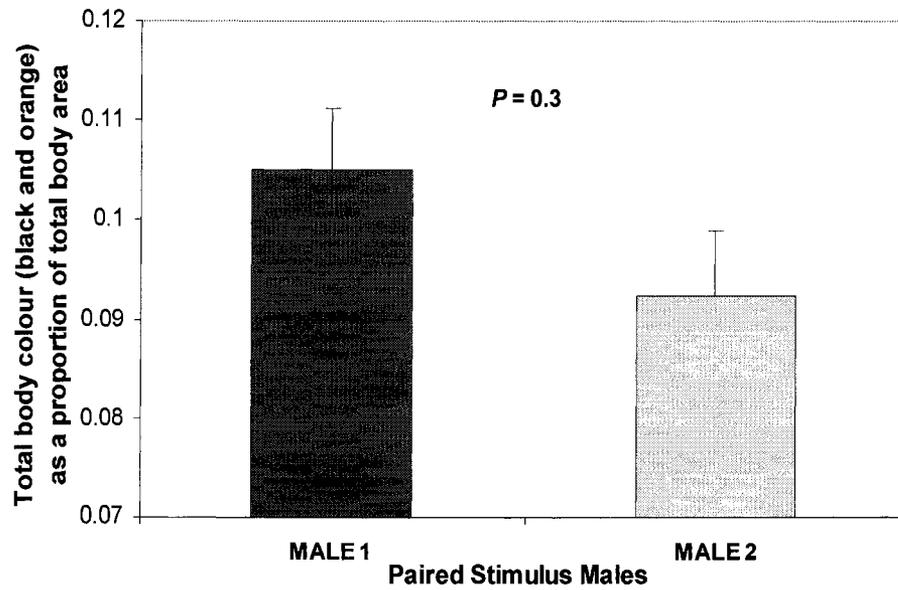
Appendix Figure 1: (a) Mean + SE body lengths (mm) of paired stimulus males within *Treatment A* (no copying opportunity), *Treatment B* (copying opportunity, familiar model female present), and *Treatment C* (copying opportunity, unfamiliar model female present) for Experiment 1. *P-values* shown were obtained using the *paired t-test*.



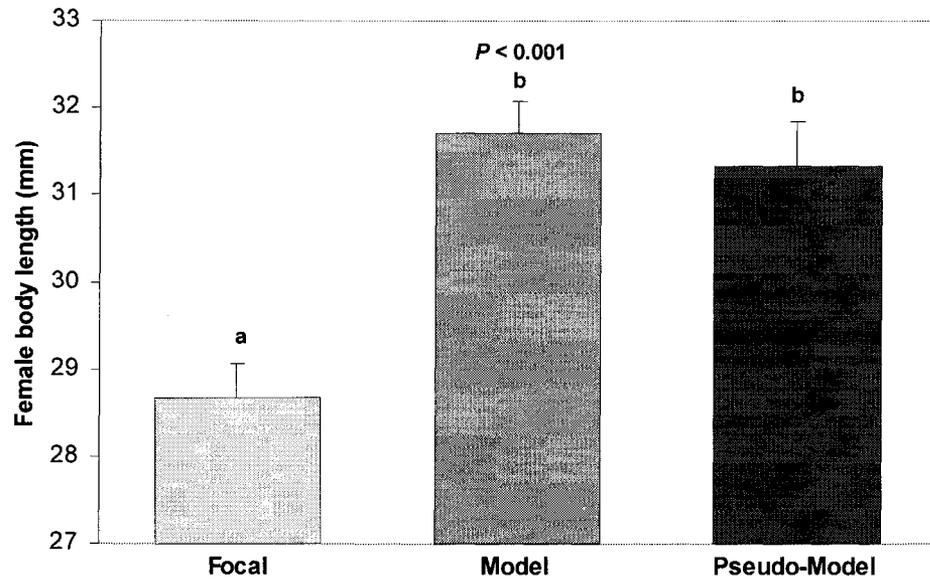
Appendix Figure 1: (b) Mean + SE total body colouration (black and orange) of paired stimulus males as a proportion of total body area (mm^2) on the left lateral side. Body colour scores are compared between stimulus males within *Treatments A, B and C* separately. *P-values* shown were obtained using the *paired t-test*.



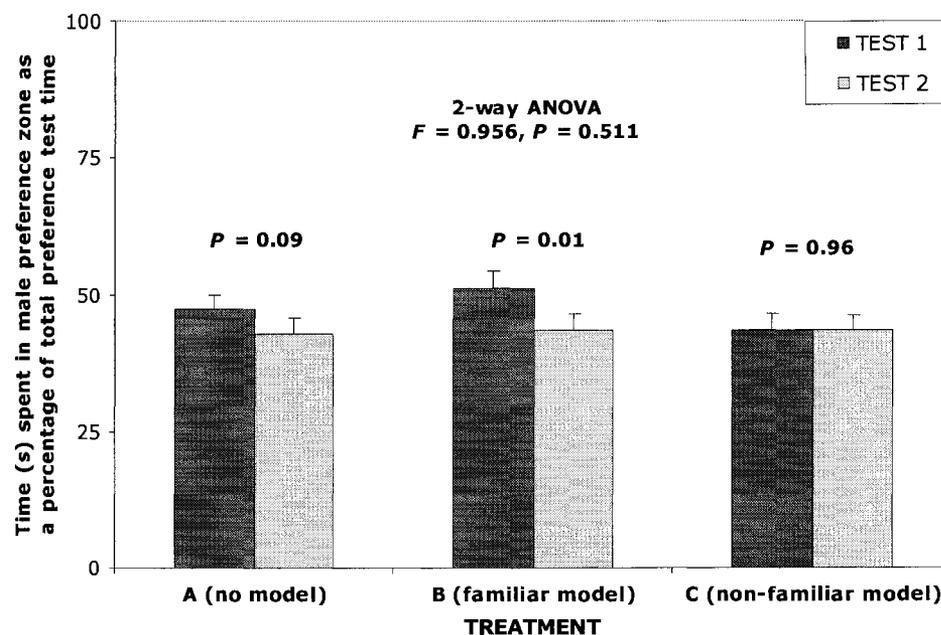
Appendix Figure 2: Mean + SE body length (mm) comparisons between paired stimulus females (*paired t-test*) and between focal, model and pseudo-model females (*one-way ANOVA*) used in the *Control Treatment* of Experiment 1.



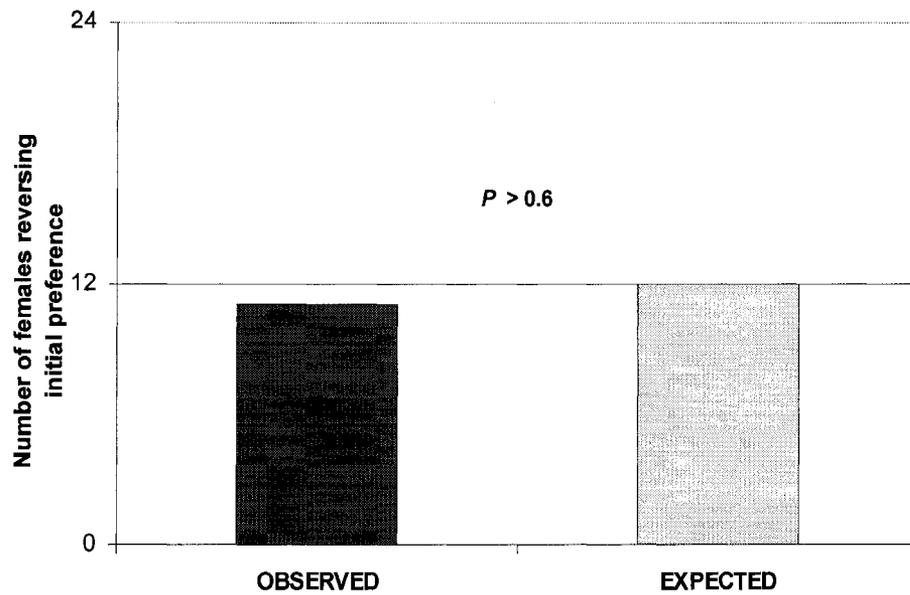
Appendix Figure 3: Comparison of mean + SE total body colouration (black and orange) as a proportion of total body area for paired stimulus males used in *Experiment 2*. *P*-value shown was obtained using the *paired t-test*.



Appendix Figure 4: Mean + SE total body lengths (mm) of focal, model, and pseudo-model females used in *Experiment 2*. *P*-value shown was obtained using a *one-way ANOVA*. Means with a similar letter above them are not significantly different from one another ($P > 0.05$), whereas means with dissimilar letters are significantly different ($P < 0.05$) from each other (*Tukey's multiple comparison test*).



Appendix Figure 5: Mean (+ SE) time (s) spent by focal females in male preference zones, near (< 7.5 cm) and facing ($0 \pm 90^\circ$) stimulus males, expressed as a percentage of the total time available in preference tests (i.e. 600 s). Values are given for both preference tests 1 and 2, and across all *Experimental Treatments* (A, B, and C) in Experiment 1. *P-values* shown were obtained using the *paired t-test* for comparing the mean percent time spent by focal females in male preference zones between tests 1 and 2, within each *Treatment* separately. *F-value* and *P-value* shown were obtained using a 2-way *ANOVA*, which compared the mean times spent by focal females in male preference zones across all three *Treatments*.



Appendix Figure 6: Number of females observed reversing their initial preference for a given stimulus female between preference tests 1 and 2 within the *Control Treatment*, Experiment 1. The expected number of reversals is based on chance (i.e. 50%; denoted by the horizontal line). *P-value* shown was obtained using the *G-test* with *Williams correction*.

CHAPTER 4

DISCUSSION

4.1 Mate-choice Copying in the Wild

This study is the first to provide empirical evidence for mate-choice copying behaviour in the guppy in the wild. While other studies have shown that female guppies will copy the mate choice of other female conspecifics in the laboratory (Dugatkin 1992, 1996a, 1998; Dugatkin & Godin 1992, 1993; Briggs et al. 1996) my results demonstrate that under natural conditions free-ranging female guppies are preferentially attracted to a male consorting with a nearby demonstrator female over a lone male, a behaviour consistent with mate-choice copying. Furthermore, the *Control Treatment* confirms that the apparent mate-choice copying behaviour observed in the *Experimental Treatment* was indeed sexually motivated, and not simply the result of shoaling with other individuals. Based on my field results, one can conclude that the previously-reported mate-choice copying behaviour of the Trinidadian guppy is not a laboratory artefact, but rather a viable alternative mating strategy within the mating system of this species.

In Chapter 2, I speculated as to why female guppies may choose to mate-choice copy in the wild, and specifically in populations originating from the Quaré River. High predation pressure in the main section of the Quaré River may promote mate-copying behaviour, as such conditions render independent mate assessment and choice risky (Houde 1997; Magurran 2005). Relatively high guppy population densities in this river (Godin 1995; pers. observation) may also contribute to the prevalence of mate copying, as these conditions should select for extensive social information exchanges between

individuals and are thus likely to facilitate copying behaviour as an alternative mate choice strategy.

To further determine whether mate-choice copying in guppies exists as a widespread natural phenomenon, additional complementary work would be necessary. While the current field study provides evidence for mate-choice copying behaviour in a relatively high-density and high-predation guppy population (Quaré River), it would be informative to conduct similar studies in other nearby rivers wherein population densities and predation pressures are lower. For example, the upper Paria River is by contrast considered a low-predation site (Magurran 2005). Upper Paria guppies may spend a greater portion of their time foraging and mate searching as opposed to evading predation risk. Consequently, the prevalence of mate-choice copying may also be lower amongst guppy populations experiencing lower-predation pressures, as the costs associated with independent assessment and choice of mates are likely lower than in high-predation populations. Likewise, in low-density guppy populations, females may generally have fewer opportunities to associate with and witness the mating decisions of other females. Accordingly, under such conditions, there may be fewer opportunities for females to mate-choice copy and instead they may resort to direct, independent mate evaluation and choice. Because local population density and predation pressure are two ecological variables known to correlate with guppy behaviour (Houde 1997; Magurran 2005), they require further evaluation with regards to mate-choice copying in order to better understand some of the additional selective forces that promote (or constrain) the expression of this behaviour in the wild. More broadly, an inter-population comparison of the prevalence of mate-choice copying in female guppies in the wild seems a fruitful

avenue for future research, and may shed more light on the selective factors that favour mate-copying behaviour in nature.

4.2 Familiarity and Mate-Choice Copying

Although I provided field-based evidence for mate-choice copying behaviour in Quaré River female guppies (Chapter 2), and Briggs et al. (1996) and Dugatkin (2007) had previously reported copying by females from this population in the laboratory, my laboratory results (Chapter 3) do not provide support for this phenomenon. The negative latter findings were unexpected and perplexing, as they led to inconclusive results with regards to my central goal of determining whether the social association (i.e. familiarity) between individuals plays an influential role in mate-copying behaviour. As a consequence, I redirected my question to assess whether the expression of mate-choice copying behaviour had been constrained under the conditions of my laboratory experiment. In my initial experiment, paired stimulus males were so closely matched in body size and colour (differing by less than 1%) that they may have been indistinguishable to focal (test) females, even in the presence of a demonstrator female. In an attempt to reduce or alleviate this potential cognitive challenge for females to differentiate between males, I re-tested for female copying behaviour in a second experiment wherein paired males were more different in body colour. Again, female preference was consistent and choice was random; the results of this second experiment were similar to those of the first experiment, and failed to provide support for mate-choice copying behaviour.

It is difficult to interpret and explain these negative results, particularly when other studies, using a similar experimental design to mine, have provided strong evidence for mate-choice copying in guppies in a laboratory (Dugatkin 1992, 1996b; Dugatkin & Godin 1992, 1998a; Godin & Dugatkin 1995; Briggs et al. 1996; Applebaum & Cruz 2000). I can only postulate as to why female preference was random in my study, and why females did not modify their initial preference to choose a male viewed consorting with a model female. Theory predicts that females, when unable to independently differentiate between males and assess their quality as potential mates, will be more likely to rely on the observed mating preferences of other nearby female conspecifics and incorporate this information into their own mating decisions (Gibson & Höglund 1992). While this reasoning is theoretically sound, in reality a female's ability to mate copy may be constrained in that she must first be able to differentiate between males, before she can further process social information provided by a demonstrator female regarding a specific male, and subsequently apply this information by copying the latter's choice of mate. If males appear to be too phenotypically similar (as may have been the case in my laboratory study), females may be faced with the cognitive challenge of having to identify, track and recollect male identity. While females may still attempt to mate copy, this cognitive challenge may impede the process.

Based on theory (Gibson & Höglund 1992) and on former work by Dugatkin (1996b) providing evidence for female mate-choice copying when males differ in orange body colour by 12% and 24% (but not by 40%), I postulated that there may be a certain range of variability in male phenotypic traits within which female mate assessment and decision-making processes would be constrained. While it is already known that females

will rely on innate mating preferences when males appear very different in phenotype (Dugatkin 1996b) (i.e. phenotypic differences exceeding some minimal discrimination threshold), and that females will copy when males differ intermediately in body colour and size (refs. loc. cited) (i.e. phenotypic differences marginally falling above this threshold), it is possible that mate-choice copying is hindered when males appear overly similar in phenotype (i.e. phenotypic differences falling well below this threshold).

To test for this possibility, I repeated the first experiment testing for mate-choice copying among familiar individuals (Chapter 2; Experiment 1, *Treatment B*), but increased the phenotypic (colouration) difference between paired stimulus males. Regardless of this modification, females still did not mate-choice copy. Because paired males still only differed by a maximum of 8% in total body colour area in this second experiment, it is possible that females were still unable to distinguish between them, and mate copying was thereby constrained. However, this is only speculation. Further experimentation is needed to better understand the influence of male phenotype on social information exchange and the degree to which it affects female mating decisions and copying behaviour.

The lack of evidence for mate-choice copying in my laboratory study may also be attributed to the physical condition and overall health of my study population (Quaré River) at large. Observed both in the laboratory and in a natural field setting in Trinidad (winter 2008), guppies originating from the Quaré River were suffering from fin rot, a bacterial condition which rapidly deteriorates the fins and has a fairly severe affect on their overall physical condition (pers. observation). Several of the wild individuals collected from the Quaré River in April 2008, and brought into a laboratory facility at the

University of the West Indies, showed obvious signs of fin abrasions and experienced unusually rapid physical health decline. Similarly, individuals collected from the Quaré River in April 2007 and returned to the laboratory at Carleton University for breeding purposes, suffered from bouts of this condition at various times. The majority of F_1 descendents that were bred and reared specifically for the purpose of my study either showed evidence of fin rot at various periods throughout their growth and ontogeny, or had been exposed to it via other infected individuals sharing their tank environment. Despite efforts to immediately treat any signs of infection with antibiotics, at least half of this population was lost, and those who survived suffered from exposure to both the bacteria and to the antibiotic treatment. Survivors who reached maturity were used in behavioural trials, but it is uncertain as to how previous exposure to sick conspecifics and antibiotics may have affected their overall behaviour.

From my recent work on the Quaré River in April 2008, it became apparent that fin rot is endemic throughout this guppy population. Observations, both in their natural riverine setting and after bringing individuals back to the local laboratory, clearly revealed this was significantly affecting overall population health and survival (pers. observation). The notable decline in the general health of Quaré River guppies over the past 10-year period (J.-G. Godin, pers. communication) is likely associated with ongoing anthropogenic ecological changes to several rivers in Trinidad. A proliferation of large-scale mining and logging operations, causing mass deforestation and soil erosion, have adversely affected Trinidadian montane forests and the wildlife within them (pers. observation). Such anthropogenic ecological disturbances may be directly linked to the declining health of local guppy populations and to the reduction in their abundances

(Magurran 2005). With any environmental effect that afflicts both health condition and survival rates of animals, their behavioural patterns may also be adversely affected. Despite the strong support for mate-copying in the wild (Chapter 2), this behaviour may be constrained under artificial laboratory conditions, particularly when individuals stem from a population exposed to certain pathogens (fin rot bacteria) that may be more virulent under laboratory conditions.

Aside from these two possibilities that Quaré females were either a) unable to distinguish between stimulus males when closely matched in phenotype, or b) suffering from altered behaviour as a result of previous exposure to endemic fin rot, there is little additional evidence to explain why females did not mate-choice copy in my laboratory experiment as expected. Nonetheless, contradicting results for mate-choice copying in guppies (and in other species) have been documented in the past. Female mating preferences, while often consistent, have also proven to be variable, depending upon phenotypic and behavioural differences expressed by males, and on physical and environmental conditions experienced by females (Dugatkin 1992; Dugatkin & Godin 1992; Godin & Dugatkin 1995; Briggs et al. 1996; Kodric-Brown & Nicoletto 1997). The origin of a population may also influence the degree to which copying behaviour is expressed. Although several studies provide support for mate-choice copying in Quaré guppies under certain circumstances (Godin & Dugatkin 1995; Briggs et al. 1996; Dugatkin 2007), the majority of evidence stems from research on populations originating from other Trinidadian rivers including the Paria River (Dugatkin 1996b, 1998; Dugatkin & Godin 1998a; Dugatkin et al. 2002; Amlacher & Dugatkin 2005; Godin et al. 2005), the Aripo River (Dugatkin 1996b), and the Ture River (Dugatkin 1992; Dugatkin &

Godin 1992). In addition, a few laboratory studies using pet-store or feral guppies have failed to demonstrate mate-choice copying behaviour (Lafleur et al. 1997; Brooks 1996, 1999). Applebaum and Cruz (2000) also found inconsistency in female mate copying behaviour in another poeciliid fish, Perugia's Limia (*Limia perugiae*), and attribute this outcome to a 'disruption effect'. Similarly, it is possible in this study that females, subjected to disruptive events in their environment, were affected in their ability to accurately process information and coherently engage in decision-making processes, which may have in turn influenced their mate preferences and choice (but see Dugatkin et al. 2003).

Based on evidence that the social environment experienced by juveniles during ontogeny can affect the manner in which they later engage in cultural information exchange and use (Dugatkin 2007), I can further speculate that the developmental conditions experienced by guppies in my laboratory population may have influenced their behaviour as adults. Dugatkin (2007) revealed that mature female guppies will only mate-choice copy when raised under social conditions that closely resemble those of their natural environment; this includes receiving either simultaneous exposure to adult females and males, or no exposure to adults at all. During development, my juveniles were raised in groups, but in the physical absence of adults; only occasionally did they receive visual exposure to adults in adjacent tanks. This aspect (along with others) of cultural priming may have impeded their ability to later exhibit mate-choice copying behaviour. It would be of interest to further investigate this developmental component, and assess whether such behaviours will vary relative to manipulations of the social context experienced during the impressionable juvenile phase.

4.3 Future Directions

Although I was not able to provide evidence for mate-choice copying behaviour in the laboratory, nor could I conclusively define whether familiarity played a role in its expression, I am confident that female guppies pay attention to sexual interactions between nearby females and males, and will copy the observed mate choices of other nearby female conspecifics when given the opportunity to do so in the wild. Despite negative laboratory results, the strong positive evidence for mate-choice copying behaviour in wild guppies reported here is novel and important.

Potential future extensions of my field results include assessing the role of social relationships, and specifically that of familiarity, in mate-choice copying behaviour in the wild. To best ascertain whether the social association between individuals affects their tendency to engage in copying behaviour, I would propose using a protocol similar to the one applied in our field study (Chapter 2), but which further experimentally manipulates the social relationship between study subjects both within and across pools. Presumably, guppies occupying a pool are likely to have more frequent social interactions and would thereby be more 'familiar' with one another than with guppies from other pools, which are likely to be 'non-familiar' individuals. By experimentally manipulating the prior social affiliation between subject and model females (i.e. whether the model female is a familiar or non-familiar individual to subject females within that pool), we would be able to test whether, and to what degree, copying behaviour varies relative to this pre-derived social association.

My principal question pertaining to the role of social associations, and specifically familiarity, in mate choice remains one of interest and pertinence. Acquiring a better

understanding of how the social relationship between individuals influences the manner in which information is conveyed between them and subsequently used in mating decisions ought to be a fruitful area for future research. From a broader perspective, such research may further demonstrate the overall importance of social information acquisition and use, and cultural information transmission, in shaping both the behaviour of individuals and behavioural interactions among individuals within social groups. Within the context of mate preferences and choice, social associations are likely to be important in shaping and directing sexual selection processes.

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