SOCIAL AND ENVIRONMENTAL INFLUENCES ON MATE ATTRACTION, MATE CHOICE AND TERRITORIAL DEFENCE



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DECLARATION

This thesis is my original work and no part has been submitted for a previous degree. I am the senior author on seven of the eight chapters presented. I am the principle contributor to the research design, data collection and analysis, written work and manuscript preparation for publication. In Chapter 6 I contributed equally with my co-author, Jessica Bolton, to all of the aforementioned responsibilities. Chapter 3 and Chapter 7 were co-authored by Catherine Hayes and Jessica Bolton respectively, both of whom contributed to the field data collection for these projects. In Chapter 5 and Chapter 8 my co-authors contributed to the statistical analysis (Andrew Kahn for both projects) and field data collection (Tim Maricic in Chapter 5 and John Hunt in Chapter 8). My supervisors, Patricia Backwell and Michael Jennions, are co-authors on all my chapters, contributing to the study conception, development of ideas, statistical analysis and advice on draft versions of my manuscripts.

With the exception of Chapter 5 and Chapter 8, which are currently submitted for publication (since the examination of my thesis these have now been accepted for publication), all the chapters of this thesis have been published in peer-reviewed journals. The bibliographic details for each of the published manuscripts are provided at the start of each chapter. No part of this thesis has been submitted for a previous degree.

In the appendix I have included a popular science article that I wrote during my PhD that was published in NewScientist and although related to my thesis topic, is not intended to be part of my main thesis.

Sophia Callander, 2012

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ABSTRACT

This thesis explores social and environmental influences on mate attraction, mate choice and territoriality across a range of model vertebrate and invertebrate species.

Chapter 1 investigates context-dependent male mate choice in the eastern mosquitofish (*Gambusia holbrooki*). Theoretical models predict that male choice is strongly influenced by the level of male-male competition. I found, however, that males associated with larger females, irrespective of the presence of rivals or these rivals' relative competitive ability. It seems, at least in this system, that males do not maximise their expected reproductive success in the immediate social setting.

In Chapter 2 I explore who is the ideal neighbour for a male during the communal courtship displays of fiddler crabs (*Uca mjoebergi*) where females can encounter males at varying distances. The initial distance at which males are seen partly determined how neighbours' sexual signals affected male mating success, suggesting that males should ideally court next to less attractive neighbours. Interestingly, fiddler crabs are also one of the few territorial species where larger (more attractive) males act to retain smaller (less attractive) neighbours by assisting them to repel intruders (defence coalitions). In Chapter 3 I show experimentally that males are indeed more likely to attract females if they court alongside smaller males.

Chapters 4 and 5 examine the role of multiple male cues, namely the display rate, size and shape of the fiddler crab major claw, during female choice. I found that female *U. mjoebergi* selected mates based directly on wave rate but also indirectly on claw size because smaller males were less likely to wave. In a separate experimental study, controlling for the colour, wave rate and size of the major claw, I show that claw shape alone plays little or no role in female mate choice in this species.

When male fiddler crabs (*U. annulipes*) lose their original major claw, they can regenerate a new one that looks nearly identical but reduces their fighting ability. In Chapter 6 I test whether claw regeneration has an effect on coalition formation. Males with regenerated claws are as likely to help their neighbours as are original clawed males. This suggests that even though males with regenerated claws are weaker competitors, they still benefit from retaining a smaller neighbour.

Chapter 7 looks at the role that resource value plays in determining fight outcome for a territory centered on a burrow in *U. annulipes*. Here, I show that when the disputed resource is also required for breeding (i.e. during the mating period), individuals with low resource holding potential (RHP) can improve their chances of mating if they escalate fights.

In the final chapter I test whether the social environment affects male advertisement calling in three populations of field cricket (*Teleogryllus commodus*). There is some evidence that males increase their calling effort in response to the presence of a rival. Males housed with a rival also experienced a significant reduction in adult longevity. My results highlight the potential importance of plastic behavioral changes in courtship by males to life history strategies.

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INTRODUCTION

Comprising eight stand-alone chapters this thesis explores some key concepts in behavioural ecology with a central focus on social and environmental factors that influence mate attraction, mate choice and male territoriality. It is primarily question driven and employs a range of suitable vertebrate and invertebrate species, namely the eastern mosquitofish (*Gambusia holbrooki*), the native Australian black field cricket (*Teleogryllus commodus*) and two species of fiddler crab (*Uca mjoebergi* and *Uca annulipes*) to investigate these questions in both a field and laboratory setting.

Testing the theory: context dependent male mate choice?

All else being equal, a male should prefer larger, more fecund females because he will then sire more offspring. A female's value, however, decreases as the number of competing males increase because paternity is then shared among several males. The presence of rivals should therefore affect male mate choice. Indeed, theoretical models for the evolution of male mating preferences predict that selection will rarely result in all males exhibiting the same preferences (Servedio and Lande 2006; Servedio 2007). In Chapter 1 I tested what happens in eastern mosquitofish (*G. holbrooki*) when a male can choose between a large and a small female in either the presence or absence of a rival. Additionally, I examined whether his choice was influenced by whether his rival was less or more competitive.

Why eastern mosquitofish?

G. holbrooki present an interesting system to experimentally test theoretical models of male mate choice. This species occurs at high densities where it is common for males to be exposed to several simultaneously available females (Zulian et al. 1995). There is no male courtship, and instead males adopt a coercive mating strategy. In the absence of competitors, males preferentially associate with larger females (Bisazza et al. 1989; Hoysak and Godin 2007; Mautz and Jennions 2011). When two or more males compete, however, most mating attempts are by the larger, more dominant male (Hughes 1985; Bisazza and Marin 1995; Pilastro et al. 1997; Bisazza et al. 2001).

Keep your enemies close: can your neighbours affect your attractiveness?

Having courting neighbours that invest more in sexual signals might increase the likelihood that a female initially approaches a displaying group of males (i.e. long-range attraction is elevated). Simultaneously however, a male should benefit from having courting neighbours that invest less in sexual signals when viewed at close range. In communally displaying species, determining what factors affect female choice at varying distances is difficult using only observational data. In Chapter 2 I experimentally investigated whether female mate choice among the same set of males differed depending on the initial distance at which the female encountered males in the fiddler crab *U. mjoebergi*.

Interestingly, fiddler crabs are one of very few territorial species where some males have been shown to influence who acquires abutting territories (Backwell and Jennions 2004; Booksmythe et al. 2010; Detto et al. 2010; for an example in another species see Elfström 1997). Males do this by forming defense coalitions with their immediate territorial neighbours: larger clawed resident males (hence superior fighting competitors; Jennions and Backwell 1996) help protect their smaller clawed neighbours against intermediate sized intruding males. Given that male fiddler crabs mainly compete with their immediate male neighbours when courting females (Callander et al. 2011), large males might gain a mating advantage by having smaller neighbours if female choice is comparative. In Chapter 3 I present a follow-up study that tested whether a male's relative attractiveness is increased when he displays alongside smaller rivals in *U. mjoebergi*.

Why fiddler crabs?

Fiddler crabs offer an ideal system to study female mate choice and male courtship behaviour. *U. mjoebergi* inhabit dense, mixed-sex intertidal communities where both sexes own a territory centered on a burrow. During the breeding season females leave their territories in search of a mate. This mate-searching behaviour induces the males in the colony to cluster together in small groups and each wave their one, greatly enlarged claw in a 'come-hither' type courtship display. Females therefore initially encounter groups of males at varying distances as they wander through the population. Previous experimental work in this species has shown that females base their mating preferences on several components of this highly conspicuous male display including claw size, wave rate, and wave leadership (Reaney et al. 2008; Reaney 2009; Milner et al. 2010a). Following mating, a female remains in a male's burrow to incubate her eggs, and several aspects of the burrow (e.g. size, temperature and stability) influence her reproductive success (*Uca genus*; Christy 1983; Christy 1987; deRivera 2005; Reaney and Backwell 2007).

Exploiting the sensory: female assessment of multiple male signals

The courtship display of fiddler crabs has an array of visual cues at its disposal, including the colour, shape, size and motion of the male's major claw. Selection for multiple male secondary sexual characteristics might have evolved to improve signal detection, species recognition and/or facilitate female discrimination of quality among males when viewed simultaneously (e.g. Brooks 1996). Although previous experimental work in *U. mjoebergi* has shown a strong preference for males with larger claws and higher wave rates, there is no observed correlation between these traits in the field. How then do females select a mate when they have mating preferences for multiple male traits? In Chapter 4 I documented whether females base their mate choice decisions on wave rate and/or claw size under natural conditions by comparing chosen males with their immediate neighbours. As colour has also been shown to be imperative during female mate choice in this species (Detto et al. 2006), in Chapter 5 I therefore investigate the final cues that females might use when choosing males, namely the shape of the claw.

Bluffing their way through: the effects of claw regeneration on male territoriality

In the next two chapters of my thesis I utilise another model invertebrate system, the African fiddler crab, *U. annulipes*. This species is closely related to *U. mjoebergi* and shares almost identical mating and territorial behaviours, including the formation of defence coalitions. As in other fiddler crab species, when a male loses his major claw (following a predation attempt for example) he can regenerate a new claw. This new claw has less muscle mass, a longer dactyl and fewer tubercles (Yamaguchi 1973; Crane 1975; Backwell et al. 2000; Lailvaux et al. 2009), consequently, males with regenerated claws are poorer fighters (Backwell et al. 2000; Reaney and Backwell 2007; Lailvaux et al. 2009). To date, studies on coalition formation in fiddler crabs have excluded males with regenerated claws, treating this as a confounding source of variation (Backwell and Jennions 2004; Booksmythe et al. 2010; Detto et al. 2010; Milner et al. 2010b). In Chapter 6 I therefore tested whether claw regeneration had an effect on coalition formation because of its potential to alter the costs and benefits of helping.

When females require a resource for breeding (e.g. a burrow) males have to successfully defend this resource in order to reproduce (review: Kelly 2008). To accrue fitness, weaker individuals must overcome their inherent strength disadvantage (lower resource holding potential; RHP) by paying higher fight costs. In *U. annulipes*, a burrow and its surrounding territory is a valuable resource used as a refuge, foraging area and water supply. During the mating period, having a burrow and territory has additional value for males because it is used as a courtship, mating and egg incubation site (Backwell and Passmore 1996). Individuals are generally prepared to pay higher costs if the benefits of winning are greater (Enquist and Leimar 1987; Tricarico and Gherardi 2010), so in Chapter 7 I compared the territory acquisition behaviour and fighting success of males during the mating and non-mating periods.

Gone but not forgotten: socially induced plasticity in male reproductive effort

Selection on male sexual traits can vary in response to social, environmental and temporal constraints. In many taxa for instance, males adjust their courtship effort when rivals are present (e.g. insects: Jia et al 2001; frogs: Rand and Ryan 1981; newts: Aragón 2009; crabs: Milner et al 2011). Geographic variation in sexually selected traits has also been well documented (e.g. guppies, Magurran 2005; damselflies, Gosden and Svensson 2008). The extent to which phenotypically plastic responses differ predictably among males, or the effects of any changes in costly courtship displays on life history traits is, however, less well studied. In the final chapter of my thesis I investigated whether the social environment, specifically the presence or absence of a rival, affects adult male reproductive effort and lifespan in three geographically distinct populations of Australian black field cricket (*T. commodus*). I also tested whether male body size (hence social dominance) influences any changes in calling effort or lifespan.

Why the black field cricket?

T. commodus provides an excellent model system for examining costly sexual signals within a life history framework. This species has a relatively short generation time, is easily maintained under laboratory conditions, and access to populations from different geographic locations and nightly acoustic recording equipment enabled me to ask interesting experimental questions. Furthermore, aspects of their acoustic calling behaviour and trade-offs in their life history traits have been widely studied. Male crickets compete for access to females by producing a long-distance advertisement call via forewing stridulation (Campbell and Shipp 1979; Evans 1988). In *T. commodus*, females prefer males that call at a higher rate and therefore male calling effort is a good indicator of his likely mating success (Hunt et al. 2005; Bentsen et al. 2006). During competitive interactions, larger males win more fights (Shackleton et al. 2005). Male calling effort is also condition dependent (Hunt et al. 2004) and tends to increase with age (Zajitschek et al. 2009; Maklakov et al. 2009; Kasumovic et al. 2012).

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