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**Evidence for individual variation and the role of personality in the assessment strategies of
Teleogryllus commodus contests**

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Abstract

Evolutionary game theory and assessment strategy models have been used to try to understand animal decision making processes during male-male contests. However, this has often led to mixed or inconclusive results. This may be due to various factors including that current analysis frameworks are unable to detect individual variation in assessment strategy use, that personality may affect assessment strategy use via underlying mechanisms/behavioural syndromes, or that animals are able to switch assessment strategies as contests escalate. However, these possible explanations for individual and population variation in contest dynamics have yet to be extensively explored. In this thesis I firstly assessed whether Australian black field crickets (*Teleogryllus commodus*) display consistent inter-individual variation (personality) in four different contexts. I then assessed whether these four behaviours are linked, forming a behavioural syndrome. The four behaviours measured were general activity, boldness in a novel environment, boldness after a predation-risk event and aggression towards a conspecific. Inter-individual variation was repeatable for general activity, boldness in a novel environment and aggressiveness, but not for boldness after a predation risk. Therefore, there was evidence for personality in *T. commodus*. However, none of the behaviours were correlated across contexts, indicating that there is no behavioural syndrome linking these four particular behaviours. Next, I assessed which assessment strategy Australian black field crickets (*Teleogryllus commodus*) use during male-male conflict, and whether there is any individual variation in the use of assessment strategy within the population. I then assessed whether *T. commodus* switch assessment strategies during contests by analysing each phase of the contest individually. Finally, I assessed whether boldness affects the assessment strategy employed by individuals during conflict. To assess the assessment strategy used by *T. commodus* I used novel methodology proposed by Chapin et al., (2019), and compared the results to those when using the more traditional methodology proposed by Taylor and Elwood (2003). The results from the Taylor and Elwood (2003) analysis were inconclusive. However, the Chapin et al., (2019) analysis clearly showed that *T. commodus* uses a mix of assessment strategies, that there is individual variation in assessment strategy use in my population of *T. commodus* and that switching of assessment strategy is possibly occurring between phases of the contest.

Boldness also did not appear to have an effect on the assessment strategy used in this population. As the first study to empirically apply the Chapin et al., (2019) methodology, my results demonstrate how the methodology can be applied to real animals and the improvements this could provide to the field. I believe this thesis demonstrates how important it may be to assess for individual variation in assessment strategy use, switching of assessment strategies between phases of conflict and the effect of personality on individual assessment strategy use, particularly in species that have previously had inconclusive results.

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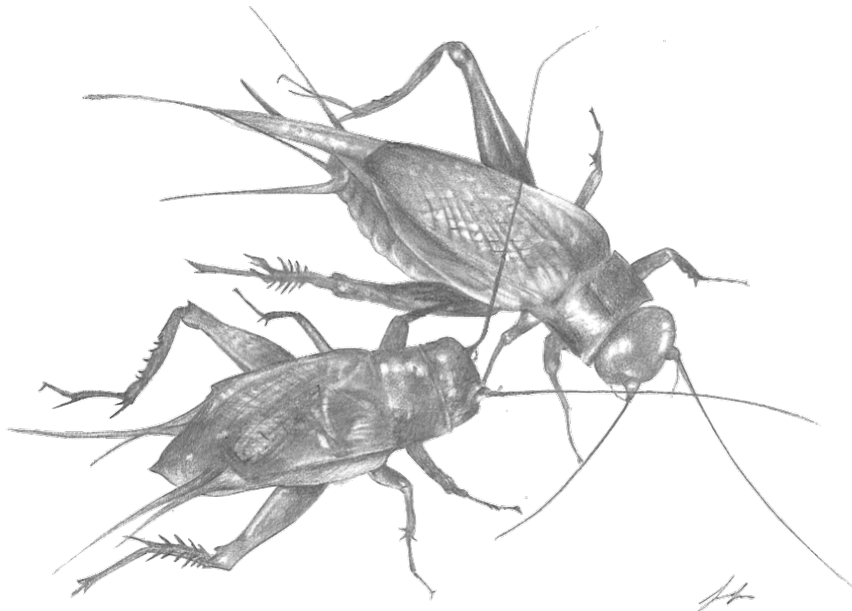
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Chapter one

General Introduction



Sexual selection and Male-Male competition

Sexual selection has been a dominant topic in biology since it was introduced by Darwin (1871). Sexual selection is an evolutionary process that drives adaptations to increase an individual's reproductive success, which often conflicts with natural selection (Hunt et al., 2009). The main mechanisms Darwin proposed through which sexual selection acts were male-male competition and female choice. Male-male competition involves males of the same species competing for access to females in order to reproduce (Darwin, 1871). Males may compete directly for ability to mate with a female, or they may compete for dominance rights, territory or resources which increase their access to females. Sexual selection therefore acts upon attributes that increase fighting success such as weaponry, size and behaviour, either by directly increasing their ability to win contests, or indirectly by providing honest signals of fighting ability and health to warn off other competitors (Andersson & Iwasa, 1996; Emlen, 2008; Kodric-Brown et al., 2006; Kodric-Brown & Brown, 2015).

Contest Strategy

Winning male-male contests increases a male's access to a female in order to reproduce successfully. Therefore we would expect sexual selection to lead to highly effective weapons and a 'total war' strategy in contests to maximise the chance of winning, causing high fatality outcomes. However, fatalities are rare, and instead 'limited war' type contests are more common, involving ineffective weapons, or highly ritualised fighting tactics that minimise serious injury are more common (Smith & Price, 1973). For example, the Arabian oryx (*Oryx leucoryx*) horns are shaped in such a way that in order to direct their horns towards an opponent during a fight they have to kneel with their head between their knees minimising the force of the blows and the potential injury they could cause (Darwin, 1871). In many snake species, male's wrestle each other, but do not use their fangs to cause injury (Shaw, 1948, 1951). Mule deer bucks (*Odocoileus hemionus*) fight vigorously when pushing their antlers together, but will not attack when an opponent has turned away and exposed unprotected areas of its body (Linsdale & Tomich, 1953). One explanation for these efficient weapons, or ritualised behaviours, is that if too many individuals were seriously or fatally injured during male-male contests, it would be detrimental to the species as a whole, which follows the assumptions of 'group selection'. Group selection, however, conflicts with

Darwin's theory of individual selection, as well our understanding of genetics which suggested that group selection would be a weak selection pressure compared to individual selection (Maynard Smith & Price, 1973). Instead, the application of game theory to animal contests has provided an explanation for the evolution of limited war type contests.

Evolutionary Game theory

Game theory is the use of mathematical models to study interactions and strategies between competing opponents (Roger, 1991). Game theory has applications in a wide range of fields and has become the umbrella term for the science of logical decision making in humans, animals and computers. Evolutionary game theory was born when John Maynard Smith realised that game theory could be used to explain animal contests and the evolution of limited war type contests benefiting both individuals and species as a whole. Maynard Smith and Price (1973) modelled five strategies which could employ three tactics and then tested whether they could be evolutionarily stable strategies (ESS), such that no mutant strategy could enter the genetic pool and produce a higher reproductive success. The three tactics were: conventional tactics that cause limited injury, dangerous tactics that could cause serious injury if used often and retreat resulting in losing the contest. The five strategies were Mouse, Hawk, Bully, Retaliator and Probe-retaliator. The hawk strategy is a 'total war' strategy while the mouse strategy represents a total peace strategy, the other three are 'limited war' strategies. Total war involves the individuals always using dangerous tactics until it wins or is seriously injured. Limited war is when the individual starts with conventional tactics but can later escalate to damaging tactics with differing probabilities, but always escalates if the opponent does. Lastly in the total peace/mouse strategy, the individual never uses dangerous tactics and will retreat immediately if faced with one. For a strategy to be evolutionarily stable it has to be the most successful in a population with a majority of the same strategy, as sexual selection will drive the gene pool to have a greater allele frequency of the most successful strategy. Hawk was shown not to be an ESS as mouse and bully strategies receive more benefits in a hawk population than hawks did. Instead, the retaliator strategy was shown to be an ESS and probe-retaliator was almost an ESS. Therefore limited war type strategies are more evolutionarily stable and provide greater benefit to individuals as well as the species.

Symmetric vs Asymmetric contests

While Maynard Smith and Price (1973) had managed to explain why limited war strategies that minimise injury have evolved, it was based on the assumption that contests were 'symmetric' where all individuals had equal fighting ability. However, in real animal contests, individuals are not always equally matched, leading to 'asymmetric' contests (Maynard Smith & Parker, 1976; Parker, 1974). There are two main causes for these asymmetric contests. The first is due to differences in the pay-off of the contest for each individual. For example, when a territory is already being held by one contestant, the invading opponent has less to lose by retreating than the territory holder which may have invested time and energy into gaining and maintaining the territory. The second is that individuals may have differences in their ability to gain or retain the contested resources, i.e. they may have differences in their fighting ability due to differences in certain characteristics such as size or health (Maynard Smith & Parker, 1976). This has been termed the resource holding potential (RHP) and it is expected that individuals with higher RHP are more likely to win contests (Parker, 1974). This raises the question of which strategies are ESSs when considering these asymmetries; are opponents able to detect information about the asymmetries/RHP and how do they use this information? Smith & Parker (1976) concluded that ESSs in asymmetric contests were those that allowed RHP cues to be used to settle contests without escalation, but escalation would occur if information to the contestants was imperfect. From there many ESS models were developed, varying in the way in which the opponents assessed RHP cues.

Assessment strategies

The four main theoretical models that have been most extensively empirically tested to understand animal contests are the war of attrition model (WOA) (Mesterton-Gibbons et al., 1996), the energetic war of attrition model (E-WOA) (Payne & Pagel, 1996), the cumulative assessment model (CAM) (Payne, 1998) and the sequential assessment model (SAM) (Enquist & Leimar, 1982). All four models assume that RHP is the main determinant of the outcome of the conflict but differ in the way in which information about the RHP is gathered. WOA, E-WOA and CAM all come under the umbrella of a self-assessment strategy which assumes that the decision to withdraw is determined by the individual's own RHP (Arnott & Elwood, 2009). In self-assessment strategies the RHP of each individual

determines a threshold of costs that the individual can incur during a conflict, and once the threshold is met, the individual withdraws from the contest. Therefore, the opponent with the greater RHP will have a higher threshold and will outlast the lesser RHP individual. The WOA and E-WOA differ in that according to E-WOA the energy used during the contest is the main cost, while the time spent in the contest is the main cost according to the WOA model (Pinto et al., 2019). CAM differs slightly from WOA and E-WOA in that it also takes into account the actions of the opponent and their effect on the individual i.e. the cost of injuries caused by the opponent are also considered a cost of the contest (Payne, 1998). In contrast, the SAM comes under the mutual assessment umbrella, which assumes that individuals are able to gather information about their opponents RHP in relation to their own RHP and will avoid conflict if they consider themselves weaker than their opponent (Enquist & Leimar, 1982). If the opponents are closely matched, then the contest will escalate to provide more information about each other's RHP and fighting ability, until one individual identifies itself as weaker and withdraws (Pinto et al., 2019).

Development of assessment strategy models

For many years it was assumed that mutual assessment (SAM) was the most common strategy used by animals during contests. This changed when Taylor and Elwood (2003) identified a statistical bias towards incorrectly assuming mutual assessment and proposed a new analytical framework. Under the Taylor and Elwood (2003) framework WOA and E-WOA models are statistically indistinguishable and therefore can be combined to form (E)WOA, which predicts that contest duration is positively correlated to loser RHP and has either a weak positive or no correlation to winner RHP. Similarly, CAM and SAM are also empirically indistinguishable when analysing randomly paired contests, both predicting a positive correlation between contest duration and loser RHP but a negative correlation with winner RHP. However, these cannot be combined as they are based on opposing assumptions and more information is required to tease apart these models (Briffa & Elwood, 2009). This information can be sourced from analysing either RHP-matched contests or the probability of escalation during contests. CAM predicts a positive correlation between contest duration and mean RHP in RHP-matched contests, whereas SAM predicts no correlation between contest duration and mean RHP (Arnott & Elwood, 2009). In contests where escalation can occur SAM predicts a negative correlation between

probability of escalation and difference in the RHP of rivals, while CAM predicts no relationship between probability of escalation and difference in RHP of rivals (Payne, 1998). While, there have been developments and improvements made to the models and the analysis of the models, there have still been inconclusive results when the models are applied to real animal contests.

Inconclusive results when applying game theory to animal contests

Despite the extensive history and many developments in evolutionary game theory and assessment strategy models, current models are still not perfect. Current empirical studies applying the theoretical models to real animals have resulted in mixed results, with most studies finding partial support for some models, support for more than one model or no support for any of the models (Arnott & Elwood, 2009; Chapin et al., 2019; Pinto et al., 2019). There are many explanations for these inconsistent results including the possibility that individuals of the same species do not always use the same assessment strategy. This could be due to differing motivation levels between individuals (Arnott & Elwood, 2009; Briffa & Elwood, 2001; Elwood et al., 2006), or due to differing personality types (Briffa et al., 2015). A population might not only differ in the assessment strategy used among individuals, but also show variation within-individuals due to past experience (Hsu & Wolf, 1999; Stuart-Fox & Johnston, 2005; Zucker & Murray, 1996) or the ability to switch assessment strategies during contests (i.e. between contest phases) (Arnott & Elwood, 2009; Hsu et al., 2008; Lobregat et al., 2019; Morrell et al., 2005; Stuart-Fox, 2006). While these have been suggested as possible explanations, they are relatively new areas of study and have yet to be extensively investigated.

Progression of the statistical analysis of assessment strategies

Another possible explanation for the inconclusive results of previous studies is limitations in current statistical analysis, especially when considering variation in the assessment strategy employed among different individuals within a population (Chapin et al., 2019). The recently proposed methodology from Chapin et al., (2019) provides a system for improving the analysis frameworks when determining assessment strategies used by species. Similar to the Taylor and Elwood (2003) framework, the Chapin et al., (2019) framework follows the prediction that under self-assessment there is no relationship between winner RHP and

contest duration, while mutual assessment predicts a positive relationship. However, the Chapin method involves repeated contest trials with focal individuals, paired with larger opponents, to ensure that the focal is the loser individual for the analysis. This allows the determination of slope of the relationship between winner RHP and contest duration for each focal individual, allowing for individual variation to be assessed. This proposed methodology could provide a significant improvement in the analysis of animal contest, however, to my knowledge it has not yet been empirically tested in any animal.

Variation in the use of assessment strategies

A major assumption of assessment strategies models is that the assessment strategy used is consistent across the species or population. However, this has been shown not to be the case, with both between and within-individual variation in assessment strategy identified in several species (Arnott & Elwood, 2009; Briffa & Elwood, 2004; Briffa & Lane, 2017; Camerlink et al., 2017; Prenter et al., 2008). In this thesis I focus on switching as a source of within-individual variation and personality as a source of between-individual variation.

Switching is the ability of an individual to use one assessment strategy in the initial phases of a contest and then switch to another strategy as the contest escalates. For example, killifish (*Kryptolebias marmoratus*) use mutual assessment when deciding whether to escalate the contest from displaying to attacking, and once the contest is escalated, the fish switch to self-assessment (Hsu et al., 2008). Similarly, male crickets (*Melanotes ornata*) use mutual assessment in the initial phase of conflict but switch to a self-assessment strategy when the fight escalates (Lobregat et al., 2019). These appear to be the only two studies that have analysed each phase of the contest separately to determine if a switch in assessment strategy occurs, although further studies have also obtained results that suggest a change from initial mutual assessment to self-assessment as contest escalate (Mesterton-Gibbons & Heap, 2014; Morrell et al., 2005; Stuart-Fox, 2006). These few studies suggest that similar results may be found when phases of contest are assessed individually in other animals.

Personality, or the consistent variation in behaviour between individuals, has been demonstrated for many behaviours across animals. Recently, it has been proposed that

personality and set behavioural traits might explain inter-individual variation in assessment strategy (Briffa et al., 2015). While a direct link between personality and assessment strategy use has not yet been studied, the link between personality and other contest aspects such as aggression, dominance, and RHP have been assessed (Briffa et al., 2015). For example proactive (bolder and more aggressive) individuals have been found to be more dominant (Colléter & Brown, 2011; David et al., 2011; Favati et al., 2014), losing fights has been shown to decrease boldness (Frost et al., 2007; Rudin & Briffa, 2012), aggression was identified as an RHP trait (Wilson et al., 2013) and shyness was shown to enhance the RHP for defenders, and winning in turn enhanced shyness (Courtene-Jones & Briffa, 2014). These studies demonstrate that links between personality and contest behaviours are possible, but the effect personality can have directly on assessment strategy use is still yet to be assessed.

Personality

Animals display differences in behavioural traits between individuals of the same species and even within the same population (Clark & Ehlinger, 1987; Magurran, 1992; Wilson, 1998). Initially, these differences were believed to be adaptive to an individual's local environments, and therefore, behavioural differences between individuals arose from differences in local environments (Dall et al., 2004). However, more recently it has been recognised that these inter-individual behavioural variations are consistent across both time and context (Gruber, 2009). These behavioural differences have been termed as personality when the behavioural variation is consistent across a single context (Dall et al., 2004), and behavioural syndromes when consistent across multiple contexts and multiple behaviours (Sih, et al., 2004a; Sih, et al., 2004b). Behavioural syndromes have had major implications for the study of animal behaviour as they indicate that behaviours are not free to evolve independently, rather they evolve as a 'package', meaning selection on one behaviour in the syndrome, may also affect all the other correlated behaviours (Price & Langen, 1992; Sih, et al., 2004b). Therefore, behavioural syndromes advocate for a holistic view of behaviours and the evolution of personality.

Assessing personality

Commonly assessed behavioural traits included activity, boldness, aggressiveness, foraging efficiency, foraging/activity after predation risk, mating behaviour and mate choice. Perhaps the most commonly assessed behavioural trait is boldness, however the actual definition of boldness has not always been consistent (Carter et al., 2013). For example, boldness has been defined as the propensity to take risks, especially in novel situations (Coleman & Wilson, 1998; Toms et al., 2010), while Réale et al., (2007) interpreted boldness as an individual's response to a risky situation itself, excluding reactions to novel situations and stimuli. Therefore, multiple tests have been designed to measure boldness, including response to novel objects, novel environments and predation risk (Carter et al., 2013). While all the tests do measure boldness they can also measure multiple traits including exploration, activity, and gregariousness, thus care needs to be taken when choosing/designing a test when assessing boldness (Carter et al., 2013). The proactive/reactive behavioural trait is also commonly assessed and involves boldness, aggression and sometimes activity being linked by a behavioural syndrome. Activity can be measured as the total time spent moving or area covered when in a familiar or novel environment (Royauté et al., 2015, 2019; Santostefano et al., 2016). Aggression is mainly measured by setting up fights between conspecifics and observing their aggressive displays (Thurmond, 1975; Wilson et al., 2010) but can also be measured by inducing aggression without using another individual via using a mirror to (Balzarini et al., 2014; Chang et al., 2020) or a decoy conspecific (e.g. Salazar et al., 2021).

Crickets as models of sexual selection, contest theory and personality research

Crickets (order Orthoptera, family Gryllidae) are often used in studies on sexual selection, contest behaviour and personality/behavioural syndromes. Many aspects of sexual selection have been studied in crickets including song (Gray & Cade, 1999; Olvido & Wagner, 2004), ageing and lifespan (Archer et al., 2012), female choice (Ritz & Köhler, 2010; Simmons, 1986) and male choice (Thomas & Simmons, 2010). Similarly many aspects of contest dynamics and aggression have been studied in crickets, including a comparison of aggression between species (Jang et al., 2008), energetic costs of contests and the effect of diet on contest/dominance (Hack, 1997; Kelly & L'Heureux, 2021), which body traits best

predict contest outcome (Hall et al., 2010; Reaney et al., 2011), and the assessment strategies used during contests (Briffa, 2008; Lobregat et al., 2019). Personality and presence of a behavioural syndrome have also been assessed in a variety of cricket species (Dochtermann & Nelson, 2014; Hedrick & Kortet, 2012; Niemelä et al., 2015; Rose et al., 2017; Santostefano et al., 2016; A. D. M. Wilson et al., 2010). The numerous use of crickets as study organisms is likely due to crickets being widely distributed globally and abundant in most areas, as well as being commercially bred in many countries for use as pets, pet food or for human consumption (Magara et al., 2021; Thomas, 2003; Weissman et al., n.d.). Therefore, crickets are highly accessible. Crickets are also invertebrates which do not have the same legal considerations required as vertebrates in research (Drinkwater et al., 2019). Thus conducting manipulative experiments with invertebrates/crickets is often easier than with vertebrates such as rodents or mammals. Invertebrates also tend to have shorter life-spans than vertebrates and can thus be bred quickly and multiple generations easily studied. Invertebrates such as crickets may also have simpler behaviours, which are more clearly linked to their metabolism and energy stores (Briffa et al., 2015), while still being complex enough for individual variation in behaviour to occur. Most cricket species tend to be highly territorial and aggressive (Alexander, 1961), thus, making crickets a good model species, not only for sexual selection, but also personality and contest theory.

The Australian Black Field Cricket (*Teleogryllus commodus*)

The Australian Black Field Cricket (*Teleogryllus commodus*) is endemic to Australia and distributed throughout Australia, New Zealand, and more recently China (G. Chen et al., 1967; Ma, Libin et al., 2015). Males attract females to their burrows by producing songs by rubbing specialised areas of the forewings together. Females have been shown to prefer males who have a high number of repeats in their song calls. This may be due to prolonged repetitive calling having a large energetic cost, therefore the ability to produce calls for a long amount of time is a good indicator of genetic superiority (Bentsen et al., 2006). Once a male has succeeded in attracting a female into his territory, the female may undergo multiple matings with the male, which involves the female mounting the male to accept his spermatophore (Shackleton et al., 2005). After a successful mating and fertilization of the eggs, the female will deposit her eggs with her ovipositor (Bonilla et al., 2015). Male reproductive success is therefore dependent on the quality of the song call, but also the

male's ability to defend the female and/or burrow from other males. Consequently, males are highly aggressive towards other males and fight to gain or retain their territory/female (Bussi gre et al., 2006). Fights follow a stereotypical sequence that starts with touching each other with their antennae and flaring their mandibles (Reaney et al., 2011). If neither male retreats, the fight then escalates to wrestling and biting until one male retreats (Reaney et al., 2011). This highly ritualised fighting behaviour as well as their willingness to fight makes these crickets an ideal species for studying contest dynamics and the assessment strategies used during conflict.

Thesis outline

In this thesis I aim to determine whether inter-individual and intra-individual variation in assessment strategy use could be caused by differences in personality types and switching of assessment strategy use between contest stages. To do so, I investigate whether personality is present in *Teleogryllus commodus*, the effect of personality on assessment strategies, and assess whether males switch strategies between contest phases. Both personality and switching may prove to be viable explanations for previous inconsistent results when applying evolutionary game theory assessment strategy models to real animal contests.

Chapter two investigates how personality may affect the fighting behaviour of Australian black field crickets. Through a set of experimental assays I assess whether the crickets have repeatable inter-individual differences (personality). I then determine whether a behavioural syndrome is present in black field crickets, linking a suite of behaviours, particularly aggression and boldness. A link between boldness and aggression may mean bolder individuals use different strategies compared to shyer individuals, providing an explanation for between individual variation in assessment strategy use.

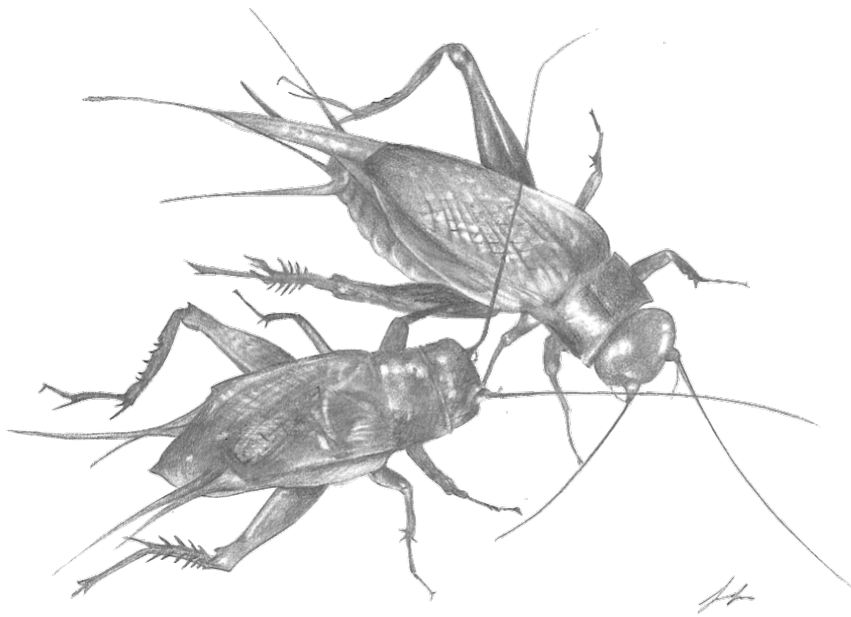
In **Chapter three** I determine which assessment strategy *T. commodus* uses, and if between and among individual variation in assessment strategy use occurs. I do this by determining the proportion of self-assessment vs mutual assessment being used in my population and whether switching of assessment strategies is occurring between phases of contest. I also follow on from chapter two by assessing the correlation between personality and the

assessment strategy used. In this chapter I also compare the Taylor & Elwood (2003) framework to the analytical framework proposed by Chapin et al., (2019) which is currently empirically untested, to assess whether the framework is more appropriate for the analysis of assessment strategies used by animals during conflict. This chapter aims to provide insight into the causes for previously inconsistent results when applying game theory to animal contests.

Lastly in **Chapter four** I summarise my findings and discuss the implications of my results in the field of animal contest research.

Chapter two

**Personality and behavioural syndrome
presence in *Teleogryllus commodus*.**



Abstract

Individuals of the same species and even within the same populations often vary in their behavioural responses to environmental challenges. This variation in behaviour is consistent across both time and contexts to form behavioural types which are heritable personality. These consistent behavioural variations may also be correlated across contexts, forming behavioural syndromes of linked behaviours via underlying genetic or physiological mechanisms. In this chapter I assess whether Australian black field crickets (*Teleogryllus commodus*) display consistent inter-individual variation (personality) in four different contexts. I then assess whether these four behaviours are linked, forming a behavioural syndrome. The four behaviours measured were general activity, boldness in a novel environment, boldness after a predation-risk event and aggression towards a conspecific. Inter-individual variation was repeatable for general activity, boldness in a novel environment and aggressiveness, but not for boldness after a predation risk. Therefore, there is evidence for personality in *T. commodus*. However, none of the behaviours were correlated across contexts, indicating that there is no behavioural syndrome linking these four particular behaviours. These findings indicate that personality is present in *T. commodus*, however, the behavioural traits assessed are not linked via a behavioural syndrome.

Introduction

Animal personality, defined as consistent inter-individual variation in behaviour, is observed in a wide variety of taxa (Dall et al., 2004; Carere & Maestripieri, 2013). Behavioural variation between individuals was previously believed to be due to adaptations to an individual's local environment. However, many behavioural variations were shown to be consistent across both time and context and not only linked to local environment and thus personality as a cause of behavioural variation was recognised (Dall et al., 2004; Gruber, 2009). Since animal personality was recognised, research into this field has gained popularity in recent decades (Gruber, 2009). Personality and behavioural syndromes studies have been applied to a wide variety of species including mammals (e.g. Anestis, 2005; Dochtermann & Jenkins, 2007), birds (e.g. Carere et al., 2005; Duckworth, 2006), reptiles (e.g. Michelangeli et al., 2019; Stapley & Keogh, 2005), fish (e.g. Bell & Sih, 2007; Colléter & Brown, 2011) and invertebrates (e.g. Johnson & Sih, 2005; Mowles et al., 2012). A common example of personality is an individual's response to startling or novel stimuli, along a continuum of bold to shy individuals (Briffa et al., 2015). The personality traits and types of individuals can affect their fitness, thereby allowing natural selection to act upon personality (Chang et al., 2017; Dingemanse & Réale, 2005).

A behavioural syndrome is defined as a suite of correlated behaviours reflecting consistent among-individual variation in behaviour in multiple contexts/situations (Réale et al., 2010; Sih, et al., 2004 a; Sih, et al., 2004 b). For example, female African penguins (*Spheniscus demersus*) that were bolder in the nest are also more likely to travel longer vertical distances when foraging (Traisnel & Pichegru, 2019), indicating that boldness and foraging behaviour are linked via a behavioural syndrome. An important implication of behavioural syndromes is the need for a holistic view of behaviour, as individual behaviours may not evolve independently, but rather as a suite or package of behaviours (Price & Langen, 1992; Sih, et al., 2004 b). This suggests that selection pressures can indirectly affect behavioural expression by acting directly upon another genetically linked behaviour, implying that behaviours are not free to adapt to be optimal in independent contexts (Bell, 2007; Sih, Bell, Johnson, et al., 2004 b; A. D. M. Wilson et al., 2010). Behavioural syndromes and their suite of linked behaviours provide an explanation for the limited behavioural plasticity observed and even the expression of behaviours that appear to be non-adaptive (Kortet & Hedrick,

2007). Therefore, personality, especially behavioural syndromes, should be considered in all aspects of animal behaviour, including habitat use, predation avoidance, foraging and social behaviour (Gruber, 2009).

In this chapter I will assess whether there is evidence for personality and a behavioural syndrome in Australian black field crickets (*Teleogryllus commodus*). *Teleogryllus commodus* are endemic to Australia and also widely distributed throughout New Zealand (Chen et al., 1967), but are also easily bred and reared in captivity, making them an ideal study species for laboratory experiments. They are also a gregarious but territorial species where males defend their burrows from other males through contests and also fight for access to the female for mating (D. J. Campbell & Shipp, 1979; Evans, 1983). While consistent inter-individual variation in behaviours such as aggression, activity and explorative behaviour, have been observed in several species of crickets including *Acheta domesticus*, *Gryllus bimaculatus*, *G. campestris* and *G. integer* (Dochtermann & Nelson, 2014; Hedrick & Kortet, 2012; Niemelä et al., 2015; Rose et al., 2017; Santostefano et al., 2016; Wilson et al., 2010) and behavioural syndromes linking aggression, exploration and activity have also been identified in *G. bimaculatus*, *G. campestris*, *G. integer* and *Teleogryllus oceanicus* (Kortet & Hedrick, 2007; Rose et al., 2017; Rudin & Briffa, 2012; Santostefano et al., 2016), the presence of a personality and a behavioural syndrome in *Teleogryllus commodus* has not yet been assessed. To assess whether Australian black field crickets display a behavioural syndrome, I first determine whether consistent inter-individual differences in activity, exploration, risk aversion are present. Then, I assess whether these behaviours are correlated, indicating the presence of a behavioural syndrome.

Methods

Study subjects and housing:

Teleogryllus commodus were sourced from the New Zealand based iNZect direct cricket farm. Crickets arrived as late instar nymphs to ensure all individuals were unmated. Males and females were separated and reared to adulthood. However, females were not used in this study and so were added to the laboratory breeding colony for a different project. The male crickets were housed individually in 15x11x5cm transparent containers with egg

carton cups as shelters and ad libitum water and food (cat biscuits). The room housing the crickets was kept at 26°C and 40-50% RH, with a 12:12 hour dark to light schedule. Cages were cleaned weekly while food, water and crickets were checked daily.

Experimental set-up:

During the daily checks, crickets that had undergone eclosion (final adult moult) had their pronotum widths measured, marked with a paint pen, and placed into groups of 2-4 individually housed male crickets, to allow for simultaneous testing (total n cricket=47). Each group consisted of crickets of similar size and age. Size was determined by measuring their pronotum width and individuals within 2mm of each other were considered similar enough to place in the same group. Age was determined by days post-eclosion and were considered similar for placing within the same group if eclosion occurred within 1 day of each other. Crickets in each group were marked with one of four paint pen colours, creating a unique identification code for each cricket. Testing commenced at 10-20 post-eclosion, to ensure that all adult behaviours were fully developed (Santostefano et al., 2016). Each group was tested three times for each personality trait, 24hrs apart.

There were four personality traits tested, each beginning immediately after the previous assay (see below). The first assay took place in the cricket's home containers, the other three assays took place in testing arenas; a clear 5L container with an opaque divider separating the two crickets (Figure 1). All assays were filmed using a Sony FDR-AX53 camera approximately 50cm above the testing area. Testing arenas and any objects used during testing were wiped down with 70% ethanol between testings. Testing occurred during the dark period, with red lights used for visibility. Crickets were then weighed after completion of the assays on each testing day. Testing took place in the same room so environmental variation could be minimized. A red light bulb was used during testing to maintain nocturnal conditions.

Behavioural tests

i. General exploration assay:

Home containers were placed under the camera with food and water removed. The crickets were left for 3min to allow for acclimation to the new surroundings and removal of the food and water. After this acclimation period cricket activity was recorded for 30min.

ii. Novel environment assay:

Crickets were transferred from the home containers into clear shelters (a 70mL sample jar), placed upright with lids on into the testing arena. The novel object (a ~5cm long leaf) was placed on the opposite side of the arena to the clear shelter. After a 3min acclimation period the shelter lid was removed and the shelter placed on its side. The trial began as soon as the lid was removed and ran for 15min.

iii. Predation risk assay:

Following the novel environment assay, the crickets were herded back into the clear shelter, the lid put back on, and the leaves removed. The shelter was then tapped with the end of a pair of forceps for ten seconds to simulate a predation risk event. After 30s the lids were removed and the shelters placed on their side. Again, the trial began as soon as the lid was removed and crickets were observed for 15min.

iv. Aggression assay:

Immediately following the predation risk assay, shelters were removed from the testing arena and after a three-minute acclimation period the opaque dividers separating the crickets were removed. The trial began as soon as the divider was removed and ran for 15min.

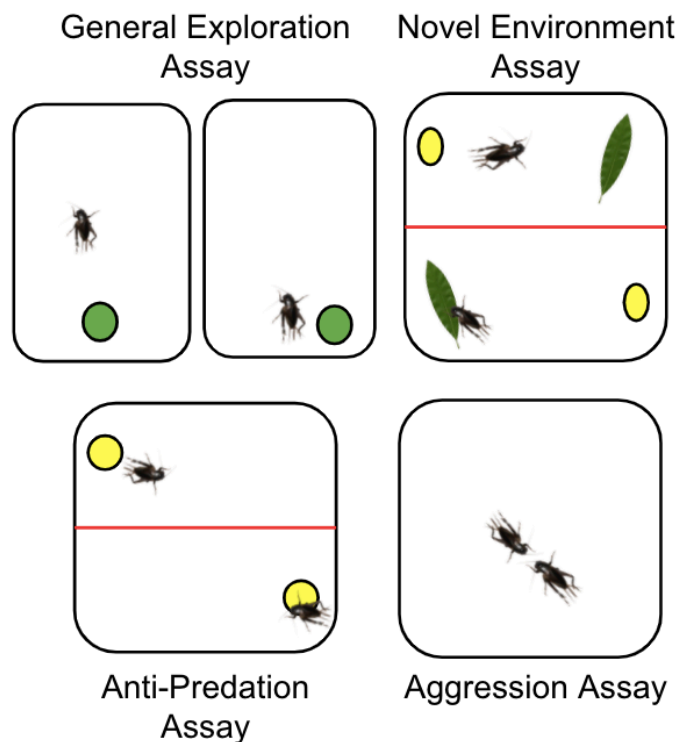


Figure 1: Diagram showing the experimental set-up of the personality assays. Green circles indicate the egg carton shelter in the cricket's home containers. Yellow circles indicate the clear testing shelters (70mL sample jar).

Video scoring and behavioural analysis

All videos were analysed using the Behavioural Observation Research Interactive Software (BORIS) (Friard & Gamba, 2016). The total time spent moving around the home container and total time spent hiding under the home shelter were measured in the general exploration assay. From the novel environment assay, the time taken for the head and then body to emerge were recorded. All limbs had to leave the rim of the shelter for body emergence to be recorded. The time taken to touch the leaf as well as the number of times the leaf was touched were also recorded. If the cricket did not emerge after 15min, it was recorded as a non-emergence. Similarly the time taken for the head and body to emerge were recorded for the predation risk assay. If the cricket did not emerge after 15min, it was counted as a non-emergence. Finally in the aggression assay the number of approaches, retreats, fights and chases of each individual were recorded. The winner and loser

individuals were also determined, mainly by identifying the winner as the individual that chased the loser, as only the winner would chase following a fight.

Statistical analysis

All statistical analyses were performed using R software v.3.6.3 (R Core Team, 2020).

To assess whether the crickets showed consistent inter-individual variation in behavioural responses across the three trials, I made univariate models for each behaviour and calculated the repeatability of each behaviour using the lme4 (Bates et al., 2015), lmerTest (Zeileis & Hothorn, 2002) and tidyverse (Wickham et al., 2019) packages with 'lmer', 'lmerTest' and 'tidy' functions. In the univariate model age, test number and body weight were included as fixed effects and cricket ID was included as a random effect. The repeatability was calculated as between-ID variance divided by the sum of between-ID variance and residual variance (Nakagawa & Schielzeth, 2010). I then made multivariate models using Markov chain Monte Carlo generalised linear mixed models (MCMCglmm) using the MCMCglmm package (Hadfield, 2010), which allows for the assessment of the between and within correlations between the behaviours. The between individual correlation is calculated as between individual covariance divided by the square root of the multiplication of the two between individual variances (Dingemanse & Dochtermann, 2013). I did two sets of multivariate model analyses: behavioural measurements in each assay (within assay correlation) and one behaviour from each assay to represent the assay (between assay correlation). The behaviours chosen from each assay, for the between assay correlation analysis were; total time spent moving, time taken to touch the novel object and total number of chases, as these were the most repeatable behaviours. In these multivariate models, I included age, test number and body weight as fixed effects and ID as a random effect. Between individual correlation was allowed, while within-individual correlation was not allowed. The priors were set as R-structure: $V=4$, $\nu=1.002$ and G-structure: $V=4$ for the within the novel environment assay analysis, R-structure: $V=2$, $\nu=1.002$ and G-structure: $V=2$ for both the within the general exploration assay and the within the anti-predation assay analysis, R-structure: $V=3$, $\nu=1.002$ and G-structure: $V=3$ for the within aggression assay. Finally for the model analysing between the assays the priors were set as R-structure: $V=3$, $\nu=1.002$ and G-structure: $V=3$. For all the models I used 13,000 iterations, burnin=3000, and thin = 10.

Results

Behavioural response

i. Effect of fixed variables; age, test and weight

Cricket behavioural responses were unrelated to age across all assays (Table 1), however, total time spent moving and hiding, time taken to touch the leaf and frequency of leaf touches in the novel environment were significantly affected by the day of testing (Table 1). Similarly, latency for head and body to emerge after the predation risk event, as well as chasing after conflict were significantly affected by body weight (Table 1).

Table 1: The effect of cricket age, cricket bodyweight and test number on all of the behavioural responses measured.

Behavioural assay	Response	Fixed effects	Estimate	SE	P Value
General exploration	Total time spent moving	Age	0.07752	0.06379	0.54240
		Test	-0.25806	0.09555	0.00772*
		Body weight	-0.69823	1.38955	0.35170
	Total time spent hiding	Age	-0.03941	0.05507	0.33850
		Test	0.24661	0.10309	0.01789*
		Body weight	-1.92043	1.20195	0.21360
	Time for head to emerge	Age	-0.01854	0.05561	0.67120
		Test	0.14728	0.10507	0.16250
		Body weight	0.12444	1.20847	0.78130
	Time for body to emerge	Age	-0.02874	0.05643	0.68500
		Test	0.17030	0.10414	0.1036
		Body weight	-0.02259	1.22619	0.8497
		Age	-0.05804	0.05722	0.9953

Novel environment	Time to touch leaf	Test	0.20427	0.10246	0.04773*
		Body weight	0.44891	1.24347	0.53560
	Frequency of leaf touches	Age	0.09036	0.05091	0.29240
		Test	-0.21558	0.10601	0.04357*
		Body weight	-0.65694	1.10642	0.41390
Anti-predation	Time for head to emerge	Age	-0.05764	0.04866	0.21010
		Test	0.09407	0.10685	0.37930
		Body weight	2.15558	1.05749	0.03586*
	Time for body to emerge	Age	-0.07671	0.05119	0.20680
		Test	0.14483	0.10389	0.16480
		Body weight	2.18735	1.11237	0.03639*
Aggression	Number of approaches	Age	0.03853	0.05465	0.93370
		Test	-0.05706	0.10368	0.58230
		Body weight	2.38134	1.18751	0.05619
	Number of fights	Age	-0.07288	0.04970	0.07204
		Test	0.01269	0.10774	0.90620
		Body weight	1.04845	1.07998	0.32480
	Number of chases	Age	0.05668	0.05703	0.65170
		Test	-0.04359	0.10026	0.66380
		Body weight	2.85078	1.23937	0.02780*

ii. Consistent individual variation in behaviours

Models including cricket ID explained the individual variation in most behaviours compared to models without cricket ID ($p < 0.05$), indicating repeatable consistent individual variation (Table 2). However, frequency of leaf touches in the novel environment assay, both latency for head and body to emerge in the anti-predation assay, and the number of fights in aggression assay were not repeatable (Table 2).

Table 2: The repeatability of each behavioural response over all three days of testing.

Behavioural assay	Response	Repeatability (95% CI)
General exploration	Time spent moving	0.495 (0.371, 0.532)
	Time spent hiding	0.238 (0.028, 0.301)
Novel environment	Time for head to emerge	0.238 (0.040, 0.300)
	Time for body to emerge	0.263 (0.084, 0.325)
	Time to touch leaf	0.295 (0.112, 0.357)
	Frequency of leaf touches	0.141 (0, 0.220)
Anti-predation	Time for head to emerge	0.092 (0, 0.190)
	Time for body to emerge	0.166 (0, 0.245)
Aggression	Number of approaches	0.234 (0.028, 0.303)
	Number of fights	0.103 (0, 0.185)
	Number of chases	0.315 (0.142, 0.368)

Correlation of behavioural responses

i. Within assay correlations:

Behaviours from the same assay were highly correlated, except for the aggression assay, in which number of fights was only weakly correlated with both number of approaches and number of chases. However, the number of chases and the number of approaches were highly correlated (Table 3). Since behaviours from the same assay were highly correlated, one behaviour was chosen to represent each assay in the between assay analysis. Total time spent moving represented general exploration, time to touch the leaf represented boldness in a novel environment, and number of chases represented aggression. Despite being correlated, anti-predation behaviours were excluded from further analysis as repeatable consistent individual differences were not detected for this trait.

Table 3: The correlation of behavioural response from within the same testing context.

	Behaviour Combinations	Correlation (95% CI)
General exploration	Time spent moving :	-0.639 (-0.823, -0.262)
	time spent hiding	
Novel environment	Time for head to emerge :	0.844 (0.704, 0.935)
	time for body to emerge	
	Time to touch leaf :	-0.783 (-0.900, -0.530)
	frequency of leaf touches	
Novel environment	Time for body to emerge :	0.855 (0.680, 0.933)
	time to touch leaf	
Novel environment	Time for body to emerge :	-0.744 (-0.911, -0.508)
	frequency of leaf touches	
Anti-predation	Time for head to emerge :	0.784 (0.553, 0.906)
	time for body to emerge	
Anti-predation	Number of approaches :	0.385 (-0.096, 0.737)
	number of fights	

Aggression	Number of approaches :	0.838 (0.637, 0.929)
	number of chases	
	Number of fights :	0.308 (-0.183, 0.652)
	number of chases	

ii. Between assay correlations:

Aggression was not correlated with general exploration ($R = -0.094$; 95% CI = -0.366, 0.411) or boldness in a novel environment ($R = 0.132$; 95% CI = -0.282, 0.563). General exploration and boldness were also not correlated ($R = -0.317$; 95% CI = -0.691, 0.062). Therefore, no behaviours from different assays were correlated (Figure 2), indicating a lack of a behavioural syndrome in this species.

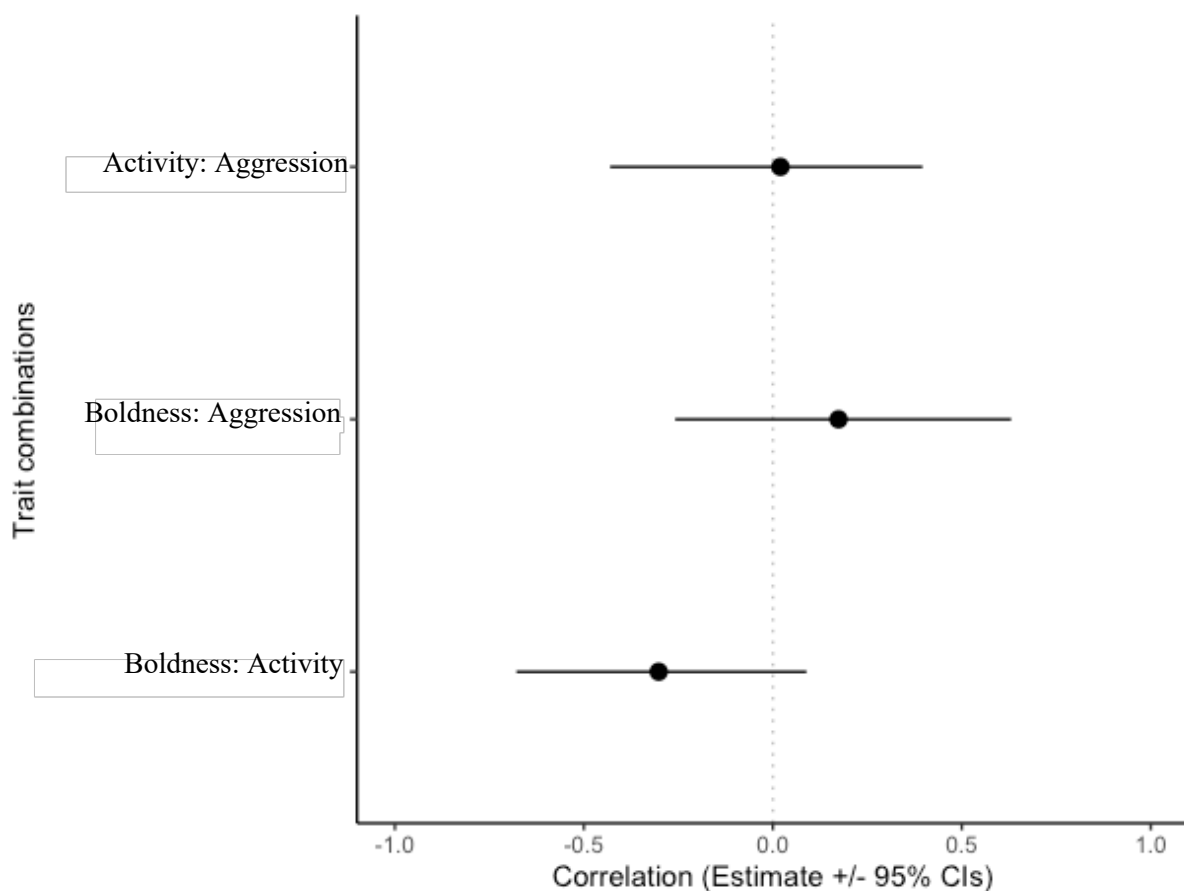


Figure 2: Correlation plot of the between-assay behavioural responses.

Discussion

This chapter investigated whether there was evidence for consistent inter-individual variation for *Teleogryllus commodus* in four different behavioural contexts and whether there was a correlation between behavioural traits. I detected consistent inter-individuals variation in three of the four behavioural assays. However, none of the behavioural responses from different assays were correlated, suggesting a lack of a behavioural syndrome linking activity, boldness, and aggression in *T. commodus*. I found that crickets showed consistent individual variation in the general exploration, novel environment and aggression assays, but not in the anti-predation assay. The presence of consistent individual differences is in line with other studies that have found evidence for personality in other species of cricket (Dochtermann & Nelson, 2014; Hedrick & Kortet, 2012; Niemelä et al., 2015; Rose et al., 2017; Santostefano et al., 2016; Wilson et al., 2010).

Repeatability of behavioural traits

Among these consistent behavioural traits identified in my study, activity (time spent moving) was the most repeatable behavioural response from all assays, with aggression (number of chases) being the second most repeatable behavioural response. This is not in accordance with the results of Bell et al., (2009) who found that aggression was one of the most repeatable behaviours across taxa, while activity was one of the least repeatable behaviours. The differences between my repeatability results compared to the results of Bell et al., (2009) could be a result of the combination between genetics and environmental factors. Firstly, activity may have higher heritability than other behavioural traits because the repeatability has been used as an upper bound of heritability. Alternatively, the higher repeatability may be a result of a positive feedback loop between the behaviour and state of the individual. For example, individuals with (stochastically and initially) slightly higher energy reserves may be more active, which leads to increased foraging success and subsequently increased energy reserves (Sih et al., 2015). In contrast, animals with stochastically lower energy reserves may be less active, leading to reduced foraging success and further reduced energy reserves and becoming less active (Sih et al., 2015). It is possible that such a positive feedback loop is more prominent for activity, and less so for other behavioural traits such as aggression.

Factors affecting the repeatability of aggression

The repeatability of aggression may also have been affected by the cricket's body weight. Bodyweight had a significant effect on the number of chases in the aggression assay, and weight has previously been shown to be correlated with exploration and aggressive behaviour, suggesting that body condition might be an underlying factor in behavioural responses (Santostefano et al., 2016). Since aggression is a social behaviour and my population were housed separately from the late nymph and adult stages, aggression may have had higher repeatability if the crickets were not housed separately and isolated, as social development may have been impacted. Social isolation during development has been shown to impact adult behaviours in both eusocial and non-eusocial insects. For example, eusocial ant (*Temnothorax nylanderi*) behaviour and brain gene expression were altered following isolation (Scharf et al., 2021) and non-eusocial cockroaches (*Blattella germanica*) reared in isolation had increased exploration-avoidance, reduced foraging activity and reduced social interaction (Lihoreau et al., 2009). However, it does not appear that social isolation has detrimental effects on territorial species such as crickets that require aggression to secure key resources (Balsam & Stevenson, 2021). Future studies could assess whether aggression has higher repeatability when crickets are housed together rather than socially isolated, despite being a territorial species.

Within-assay correlations of behavioural responses

Behavioural responses from the general exploration and novel environment assays (i.e. time spent moving and time taken for head to emerge) were correlated to the other behavioural responses that I measured from the same assay. Any of the behavioural responses from the general exploration and novel environment assays are good indicators of the behavioural trait being tested. The correlation of behavioural responses within assays provides a good indication that the assays are testing the same behavioural trait (Campbell & Fiske, 1959; Carter et al., 2013). However, for the aggression assay, the number of approaches and the number of chases per individual, were highly correlated with each other but were weakly correlated to the number of fights each individual had during the assay. This can be explained as the number of fights is dependent on both crickets involved in the contest rather than purely dependent on the focal cricket. Therefore, this suggests that the number of times an individual approaches or chases its opponent is a good indicator of aggression,

while the number of fights an individual is involved in is a poor indicator of aggression as it involves both parties. Even though I detected positive behavioural correlations within assays, the behavioural correlation between assays is not clearly correlated, suggesting that the assays are indeed testing different behavioural traits (Carter et al., 2013). Therefore it appears that the four assays were appropriate for testing activity, boldness, anti-predatory behaviour and aggression. Because most behavioural responses from the same assay are correlated, it was appropriate to select one behavioural response to represent the behavioural trait being assessed for the between assay correlation analysis.

Presence of a behavioural syndrome linking behavioural traits

While I found evidence for personality in *T. commodus*, there was no evidence for a behavioural syndrome linking activity, boldness and aggression. This does not align with the results of previous cricket studies which found correlations between behavioural traits in *G. bimaculatus* (Balsam & Stevenson, 2021; Rose et al., 2017), *G. campestris* (Santostefano et al., 2016), *G. integer* (Kortet & Hedrick, 2007) and *Teleogryllus oceanicus* (Rudin & Briffa, 2012). However, previous studies found similar evidence for personality but not for a behavioural syndrome involving aggression being correlated with boldness, exploration and/or antipredatory behaviour (Niemelä et al., 2012; Wilson et al., 2010). I did not include the anti-predation behavioural response in the between assay correlation analysis, despite the behavioural responses being correlated, as cricket identification did not have a significant effect on the behaviours, indicating that there is no significant inter-individual variation and would therefore not be subject to a behavioural syndrome. The lack of evidence for a behavioural syndrome in *T. commodus* linking activity, boldness and aggression suggests that they are not controlled by the same physiological or genetic mechanisms and are therefore not constrained, allowing for selection to shape each behaviour independently (Bell, 2007; Sih, Bell, Johnson, et al., 2004 b; A. D. M. Wilson et al., 2010). Although my results indicate that there is not a behavioural syndrome involving activity, boldness and aggression, that may not mean that there is no behavioural syndrome present at all in *T. commodus*. Future studies could assess whether a behavioural syndrome involves other behaviours, such as foraging efficiency (Tan et al., 2018), foraging after predation risk (Dammhahn & Almeling, 2012; Eccard et al., 2020), calling activity (Brown et al., 2006) and mating behaviour or mate choice (B. Chen et al., 2018; David & Cézilly, 2011).

Domestication and Lab vs Field studies

The lack of consistent individual variation in the anti-predation assay as well as the lack of a behavioural syndrome, could be due to domestication weakening the response of *T. commodus* to perceived predator presence. My population of *T. commodus* has been commercially lab bred in captivity, fed ad libitum and exposed to a virtually predator-free environment for many generations. Therefore, this population has likely experienced very different inbreeding, natural, sexual and artificial selection pressures than wild populations of *T. commodus* (Wilson et al., 2010). As has been shown in three-spined sticklebacks (*Gasterosteus aculeatus*), consistent individual differences can be generated in anti-predation behaviour when exposed to strong predation pressure (Bell & Sih, 2007). The same study found that strong predation pressure also induced a correlation between aggression and boldness (Bell & Sih, 2007). This suggests my results may not be applicable to wild *T. commodus* populations and that the behavioural responses measured may reflect a domestication syndrome (Wilson et al., 2010). Therefore, future studies might need to test the anti-predation behaviour when rearing crickets under the (perceived) predation risk in order to have consistent inter-individual variation in anti-predation behaviour. Similarly future studies using wild caught populations in the lab or directly observing wild populations in the field may indeed find that there is a behavioural syndrome linking boldness and aggression. Care must also be taken when applying the repeatability of the behavioural responses of my cricket population to wild populations or field studies as behaviours tend to have higher repeatability in the field than in the lab for several taxa (Bell et al., 2009). Therefore my results may not be directly comparable to field studies.

Effect of previously winning or losing and dominance

Prior experience can affect the behaviour of individuals during contests. Winning and losing previous contests can have carryover effects on subsequent fights with winners becoming more aggressive and thus more likely to win, while losers become more avoidant and more likely to lose (Ginsburg & Allee, n.d.; Hsu et al., 2006; Kar et al., 2016). Although I allowed 24 hours between assays to minimise carryover effects, it is possible that winning or losing the first contest may have affected the behavioural responses in the second and third day of testing. Furthermore, the level of aggression expressed by the opponent can have an impact

on the aggression expressed by the focal individual (Santostefano et al., 2016). Focal individuals may react to an aggressive opponent with reciprocal aggression, however if aggression reflects dominance, then a focal individual may only react with aggression towards a more subordinate opponent (Santostefano et al., 2016). Changes in dominance status have been shown to affect other behaviours including boldness and activity (Rudin et al., 2017). Prior experience effects in another cricket species (*Gryllus bimaculatus*) have been shown to disappear entirely after 24hours (Khazraie & Campan, 1999). However, if this is not the case for *T. commodus*, and there are carryover effects of previous contests and aggression does reflect dominance, then the effect of winning or losing may not just impact future contests and the aggression behavioural response but also the other behavioural responses being measured and the correlation between the behaviours.

A post hoc analysis of my data interestingly showed that the experience in test 1 predicts change in aggression in both test 2 (Linear regression: $\beta = 2.871$, $SE = 1.297$, $p = 0.0339$) and test 3 ($\beta = 4.611$, $SE = 1.888$, $p = 0.0201$). Similarly, experience in test 2 predicts aggression in test 3 (Linear regression: $\beta = 3.907$, $SE = 1.427$, $p = 0.0091$). Interestingly aggression (number of chases) decreased from test 1 to test 2 and test 3, with less chasing being required to win in test 2 compared to test 1 (Linear mixed effects regression: $\beta = 9.511$, $SE = 1.835$ and $p < 0.0001$). However, the same amount of chasing was required to win in test 2 and test 3 (Linear mixed effects regression: $\beta = 1.455$, $SE = 3.498$ and $p = 0.681$). This suggests that aggression does reflect dominance status and more dominant males are more aggressive and more likely to win in the first test, but that less aggression is required to continue winning in subsequent tests. This may be due to subordinate males becoming even more submissive after a losing experience, thus requiring less aggression from a dominant male to win the contest. Therefore, there does appear to be some carryover effects of previous contests, but it does not seem to affect dominance status and therefore may not affect the other behaviours also being measured.

Effect of habituation on behavioural responses

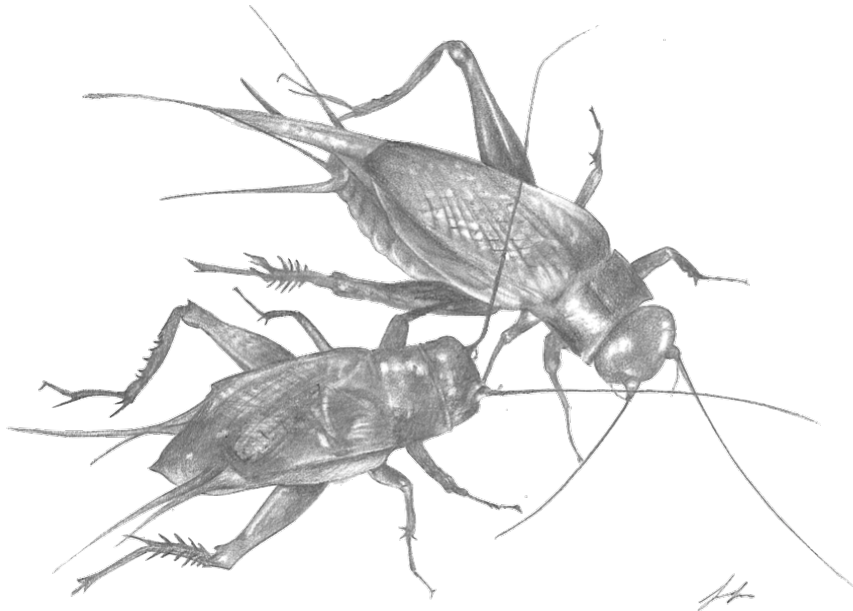
Test number had a significant effect on total time spent moving and hiding, time taken to touch the leaf and frequency of leaf touches in the novel environment assay. These behavioural changes may indicate that some habituation occurred, particularly to the novel

object. Although 24 hours was allowed between testing, it may not have been enough time to avoid habituation. As the crickets were exposed to the same stimuli, testing environment and novel object each time, they are able to familiarise with the environmental stimuli and therefore the novelty is decreased with each trial. Therefore, the potential boldness (risk-proneness) expressed decrease with each trial. However, previous studies involving other cricket species did not show habituation (Brown et al., 2006; Santostefano et al., 2016; Stahlschmidt et al., 2014). Of particular note is the study by Santostefano et al., (2016) which ran the behavioural trials over 12 consecutive days, but the 24 hour period between trials appeared to be long enough to mitigate any habituation. However, in this study they assessed exploration rather than boldness, therefore perhaps my results are due to habituation to novelty itself, as this has been demonstrated to occur (Martin & Réale, 2008; Tan et al., 2018; Wong et al., 2010). Future studies could use a different novel object (e.g., a different leaf type) or novel environment (e.g. a different testing arena or substrate) in each trial to minimise familiarisation, or allow a longer period between trials, to try and avoid habituation to the novelty itself.

In summary, while I found evidence for personality in *T. commodus*, there was no evidence for a behavioural syndrome linking aggression to other behavioural traits such as boldness and activity. These findings suggest that personality may not have influenced other contest behaviours such as the assessment strategies used during conflict. However more investigation is required, and this will be further assessed in Chapter 3.

Chapter three

Individual variation in contest assessment strategies and the role of personality



Abstract

Evolutionary game theory and assessment strategy models are used to understand decision making processes during male-male contests. However, this has often led to ambiguous results, making it difficult to conclusively assign the correct assessment model to a particular species. This may be due to various factors including that current analysis frameworks are unable to detect individual variation in assessment strategy use, that animals are able to switch assessment strategies as contests escalate, or that personality may affect assessment strategy use via underlying mechanisms/behavioural syndromes. In this chapter I assess which assessment strategy Australian black field crickets (*Teleogryllus commodus*) use during male-male conflict, and whether there is any individual variation in the use of assessment strategy within the population. I then assess whether *T. commodus* switches assessment strategies during contests. Finally I assess whether personality, specifically boldness affects the assessment strategy employed by individuals during conflict. I used the methodology recently proposed by Chapin et al., (2019), and compared the results to those when using the currently widely used methodology proposed by Taylor and Elwood (2003). Using the Chapin et al., (2019) framework I was able to demonstrate that a mix of assessment strategies are used by *T. commodus* and that individuals may switch assessment strategy between contest phases. In contrast, the results from the Taylor and Elwood (2003) analyses were inclusive and could not determine if switching was occurring. Variation in boldness did not influence the assessment strategy used. My results demonstrate the importance of individual variation, switching of assessment strategies and personality when assessing contest dynamics.

Introduction

Animal contests over limited resources such as potential mates or territories, are common across many species (Hardy, & Briffa, 2013). The winner of such contests is usually the individual with the greater fighting ability, termed the resource holding potential or RHP (Parker, 1974). However, contests rarely end in serious injury or fatality, indicating that the contest outcome is determined by the loser's decision to withdraw, rather than the winner incapacitating the loser. There is some debate around how exactly RHP is involved in the withdrawal decision making process. The main division in opinion is in the way animals assess RHP to inform their decisions. One theoretical possibility, called self-assessment, proposes that individuals decide to withdraw from a contest based only on the costs to their RHP (Payne, 1998; Payne & Pagel, 1996). In contrast, mutual assessment suggests that individuals assess the RHP of their opponent relative to their own and will withdraw once the individual perceives that it is weaker than their opponent (Enquist & Leimar, 1982). Both theoretical ideas have been tested on real animal contests, leading to empirical support for both self-assessment and mutual assessment. However, in some species the results are inconclusive, suggesting that the mechanism by which rivals make decisions during conflict is still not fully understood.

Many models based on evolutionary game theory have been used to describe the assessment strategies adopted by animals during contests. The four main empirically tested models can be divided into three categories. The 'War of Attrition' (WOA) and 'Energetic War of Attrition' (E-WOA) both fall under self-assessment (Mesterton-Gibbons et al., 1996; Payne & Pagel, 1996). WOA only considers time spent in the contest as a cost, while E-WOA also considers the energy used during the contest as a cost. However, both assume that individuals base their decision to withdraw from conflict when they reach a threshold of accumulated costs determined by their RHP. Therefore, individuals with lower RHP will reach their threshold faster, withdraw and lose the fight. The 'Cumulative Assessment Model' (CAM) is based on self-assessment and also assumes that individuals withdraw once a threshold of costs is reached, but injuries inflicted by the opponent are also considered a cost, and therefore, according to CAM individual decisions also depends on the opponent's RHP (Payne, 1998). Lastly, the 'Sequential Assessment Model' (SAM) is based purely on mutual assessment and assumes that individuals are able to gather information about their

opponents RHP in relation to their own RHP during the conflict and will quit the fight if they consider themselves weaker than their opponent (Enquist & Leimar, 1982). Since information gathering of the opponent is not perfect, especially when the opponents are closely matched, the contest will often escalate to allow the rivals to gain more information about each other's RHP and fighting ability, until one individual identifies itself as weaker and withdraws (Pinto et al., 2019).

Since it was introduced, the analysis framework proposed by Taylor and Elwood (2003) has been the most common approach for investigating assessment strategies and decision rules in animal contests. Under this framework the WOA and E-WOA models are statistically indistinguishable and therefore can be combined to form (E)WOA, which predicts that contest duration is positively correlated to loser RHP and has either a weak positive or no correlation to winner RHP. Similarly, CAM and SAM are also empirically indistinguishable when analysing randomly paired contests, both predicting a positive correlation between contest duration and loser RHP but a negative correlation with winner RHP. However, these cannot be combined as they are based on opposing methods, and more information is required to tease apart these models (Briffa & Elwood, 2009). This framework also assumes that all individuals use the same assessment strategy and may not accurately demonstrate what is really happening in a population.

The testing of assessment models to animal contests has led to mixed or inconsistent results with most studies finding partial support for some models, support for more than one model or no support for any of the models (Arnott & Elwood, 2009; Briffa & Elwood, 2009; Chapin et al., 2019). There are many explanations for these inconsistent results including the possibility that both between and within-individual variation in assessment strategy use is occurring. Between-individual variation could be due to differing personality types, which have been shown to cause variation in many other behaviours (e.g. Favati et al., 2014; Sneddon, 2003; Westneat et al., 2013; Wilson et al., 2010), or limited statistical analysis when applying the models (Briffa et al., 2015; Chapin et al., 2019). The Taylor and Elwood (2003) framework is limited by its ability to only assess species at the population level and therefore cannot detect individual variation in assessment strategy use. Recently, Chapin et al., (2019), introduced a new analysis framework which focuses on three main aspects: the

individual, its opponent and the contested resource. In this framework assessment strategies do not have to be fixed within a population, individual or contest. The Chapin et al., (2019) framework also requires the contests to be set up differently to the Taylor and Elwood (2003) framework. While both winner and loser RHP against contest duration are assessed in the Taylor and Elwood (2003) framework, Chapin et al., (2019) focuses only on the relationship between loser RHP and contest duration. However, they assess this relationship over repeated trials for each focal individual (i.e., each focal individual participates in multiple fights with an opponent of higher RHP). Although this newly proposed framework is promising for its ability to assess between-individual variation in assessment strategy use it has not yet been empirically tested. Personality as a cause of between-individual variation leading to mixed strategy use, has also been suggested but not yet assessed (Briffa et al., 2015; Pinto et al., 2019). Within-individual variation may be due to switching of assessment strategies between phases of contest (Hsu et al., 2008; Lobregat et al., 2019); this too has been rarely tested. While between-individual variation, and mixed use of assessment strategies within a population have been suggested as an explanation for inconclusive results, it has yet to be investigated (Chapin et al., 2019). Both the Taylor and Elwood (2003) and the Chapin et al., (2019) frameworks will be used to each phase of contest individually and assess whether switching is occurring.

Teleogryllus commodus are an ideal study species to investigate variation in contest strategies. They are a gregarious but territorial species where males defend their burrows from other males through contests and also fight for access to the female for mating. Importantly, the fights follow a stereotypical sequence that starts with touching each other with their antennae and flaring their mandibles (Reaney et al., 2011). If neither male retreats, the fight then escalates to wrestling and biting until one male retreats (Reaney et al., 2011). Body size appears to be a good indicator of RHP for *T. commodus* as it has previously been shown to be a strong indicator of contest outcome (Reaney et al., 2011). This highly ritualised fighting behaviour, their willingness to fight in a controlled captive setting, and the ability to be easily reared and housed in a lab, makes these crickets an ideal species for assessing contest dynamics.

In this chapter I will first determine which assessment strategy male *T. commodus* crickets use during contests and whether all individuals in the population use the same strategy. Secondly, I will analyse each phase of the contest separately to determine the assessment strategy used during each phase and whether a switch in assessment strategies between phases is occurring. For each of these steps, I will compare two different analysis frameworks (Chapin et al., 2019; Taylor & Elwood, 2003), to assess whether the novel Chapin et al., (2019) framework can provide a greater insight into contest behaviour and improve our understanding of contest dynamics. Since the Chapin et al., (2019) analysis requires repeated testing of individuals, my experimental set up involved focal individuals facing a range of randomly chosen opponents, all of which were larger than the focal individual, to ensure the focal individual loses the contest. As the Chapin et al., (2019) methodology has not yet been empirically tested, it is unclear whether it is statistically possible to determine variation within the population. Therefore, I conducted an additional simulation to determine whether it is statistically possible and what the predictions are if individual variation is occurring. Lastly, I determine whether personality explains between individual variation in the assessment strategy used. To do this I determined the boldness level of the focal individuals and then assessed the relationship between boldness and assessment strategy used. Although there was no evidence for a behavioural syndrome linking boldness and aggression in *T. commodus* (chapter 2), I predict that boldness may be correlated with assessment strategy use, as it has previously been linked to dominance and RHP (Courtene-Jones & Briffa, 2014; Colléter & Brown, 2011; David et al., 2011; Favati et al., 2014).

Methods

Study subjects and housing

Teleogryllus commodus were sourced from the New Zealand based iNZect direct cricket farm. Crickets arrived as late instar nymphs, and males and females were separated and reared to adulthood to ensure all individuals were unmated. The male crickets were housed individually in 15x11x5cm clear containers with egg carton cups as shelters and ad libitum water and food (cat biscuits). The room housing the crickets was kept at 26°C and 40-50% RH, with a 12:12hr light to dark schedule. Cages were cleaned weekly, while food, water and

crickets were checked daily. Females were added to the Invertebrate Behavioural Ecology (IBE) laboratory breeding colony for a different project.

Experimental set-up

During daily checks, crickets that had undergone eclosion were weighed (to 0.001g) and assigned an identification number. Once most of the crickets had reached adulthood, 31 focal crickets were randomly chosen (using a random number generator) and marked with a yellow paint pen.

Personality assay

To investigate the relationship between personality and assessment strategy use I first ran a series of novel environment assays to determine the boldness for each focal cricket. Personality testing for focal individuals commenced on day 10-20 post-eclosion. Each focal cricket underwent a personality test involving a novel environment assay, which included a novel object. Each assay occurred three times, 24hrs apart. Crickets were transferred from the home containers into clear shelters (a 70mL sample jar), which were placed upright with lids on and into the testing arena. The novel object (a ~5cm long leaf) was placed on the opposite side of the arena to the clear shelter. After a 3min acclimation period the shelter lid was removed, and the shelter placed on its side. The trial began as soon as the lid was removed and ran for 15min. All testing took place in a testing arena, which was a clear 5L container with an opaque divider separating the two crickets. Two testing arenas were used, to allow for simultaneous testing. All assays were filmed using a Sony FDR-AX53 camera placed ~1m above the testing area. Testing arenas and novel objects were wiped down with 70% ethanol between testings to remove any chemical scents left behind. Testing took place in the same room that housed the crickets, so environmental variation could be minimized. I chose the novel environment assay to assess boldness as the behavioural responses were repeatable, unlike the anti-predation assay and were correlated indicating that this assay is appropriate for assessing boldness (see Chapter 2).

Contest assay

To determine the assessment strategy used at the population and individual level of *T. commodus* and whether switching of assessment strategies was occurring, I set up contest

assays. Contest assays began 24hrs after the conclusion of the personality testing. Each focal cricket was paired with five different opponents, allowing for 24hrs between contests (Figure 3). The focal cricket and its opponent were placed in the testing arena, separated by the divider. After a three-minute acclimation period the divider was removed. The trial began as soon as the divider was removed and ran for 10min. The opponent that the focal individual fought each day was randomly chosen, while still ensuring that the opponent is larger than the focal. If crickets did not fight after 10min, the fight was excluded from the analysis. After, the contest was removed from the pool of opponents and either euthanised by freezing or added to the IBE lab breeding colony. The same testing arenas as the personality assays were used and wiped down with 70% ethanol in between tests.

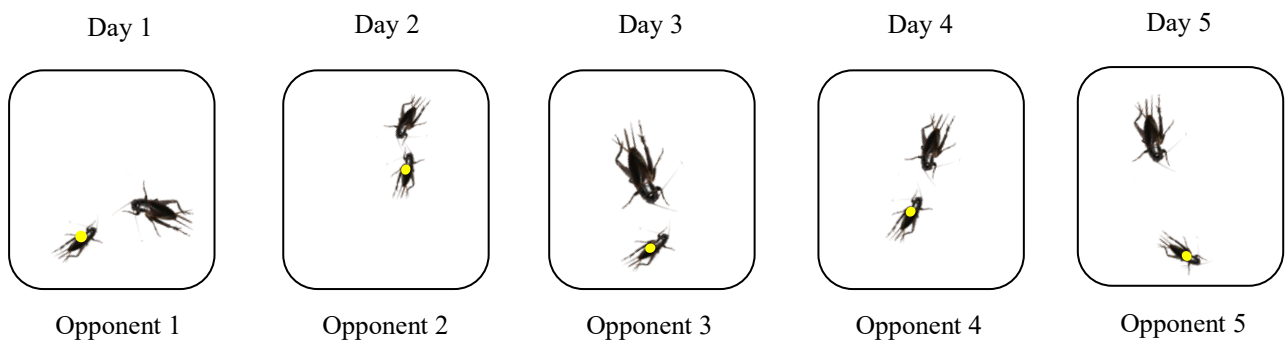


Figure 3: Diagram of the experimental set-up for the contests between one smaller focal male (indicated by yellow dot) and its five larger opponents.

Video scoring and behavioural analysis

All videos were analysed using the Behavioural Observation Research Interactive Software (BORIS) (Friard & Gamba, 2016).

For the personality assay the time taken for the body to emerge was recorded. All limbs had to leave the rim of the shelter for body emergence to be recorded. The time taken to touch the leaf was also recorded. If the cricket did not emerge after 15min it was recorded as a non-emergence.

In the contest assays, a fight was considered to have begun as soon as the antenna of one individual touched the other individual and the fight was considered to have ended once one individual retreated more than 10 cm away and remained away for at least 1 min (or

was chased away continuously by the other individual). During the contests there was a very clear distinction between the two phases (Table 4, Figure 4). Phase one began with the crickets approaching and touching each other with their antennae and orienting themselves to face each other, then if escalation to phase 2 occurred the crickets lunged towards each other and grappled each other with their mandibles and front legs. While the opponents may at points separate, if they came back together (i.e., neither cricket retreated), the contest always immediately escalated back up to phase 2. The total contest duration, whether the contest escalated from phase 1 to phase 2, the duration of each escalation phase, and the winner and loser individuals were all recorded.

Table 4: Ethogram of Contest Escalation Phases for Teleogryllus commodus

Escalation phase	Behaviour	Description
Phase 1	Antennal touching	Crickets approach each other and contact their opponent's body or antennae with their own antenna.
	Orientation	Crickets will turn their bodies to be (if not already) facing each other directly.
Phase 2	Mandible interlocking	The crickets lunge towards each other, lock their mandibles together. and grapple with their front legs.
	Wrestling	Crickets will use their front legs to grapple with each other. Biting of the front legs with the mandible and kicking each other may also occur.

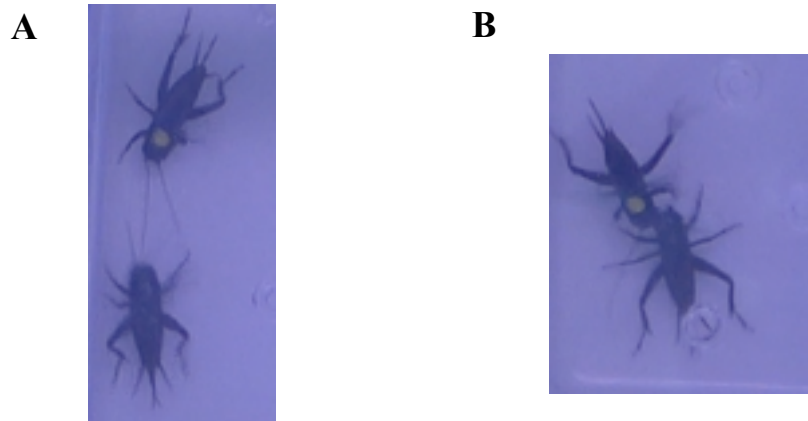


Figure 4: Images depicting (A) phase 1 and (B) phase 2 of *Teleogryllus commodus* contests

Statistical analysis

All statistical analyses were performed using R software v.3.6.3 (R Core Team, 2020).

i. Traits associated with fighting ability

A subset of individuals from the population were frozen after their contests and had their body measurements taken. From this subset, 42 individuals could be compared to the focal cricket as it was also frozen. The body measurements from these 42 crickets were calculated relative to their focal cricket and used for the trait analysis. To assess which trait best predicts fighting ability, Generalised Linear Models (GLMs) were fitted, using the ‘glm’ function in base R. I used a binomial error distribution where losing = 0 and winning = 1 as the response variable. Individual models were fitted for each body measure (body weight, body length, hind femur length and pronotum width) as an explanatory variable. The relative measures (i.e., the difference between the focal individual and the opponent) for each opponent’s trait were calculated and then used for further analysis. Akaike Information Criterion corrected for small samples (AICc) was then used to determine which model best described the relationship between the trait and probability of winning and should be used as a proxy for RHP in all subsequent analysis.

ii. Assessment strategy identification: Taylor and Elwood (2003) framework

To assess the population-level relationship between fighting ability (RHP) and contest duration, Linear Mixed Effects models (LMMs) were fitted using the lme4 package and 'lmer' function. The explanatory variable was the trait identified as the best predictor of probability of winning in the previous step, body weight, was used as a proxy for RHP, and contest duration was the response variable, focal cricket ID and trial number were included as random effects. Two separate models were made for winners and losers. Likelihood ratio tests were then performed using package lmerTest and 'lmerTest' function (Zeileis & Hothorn, 2002). Due to unforeseen deaths, not all focal crickets fought all five opponents (i.e all 27 focals fought at least twice, 23 fought 3x, 15 fought 4x and 8 fought all five opponents), therefore total number of fights = 152.

iii. Simulation model for assessment strategy identification

The approach suggested by Chapin et al. (2019) to determine the assessment strategy of each focal individual assumes that the population is necessarily composed of individuals performing different strategies (i.e., a mixed population composed of both mutual and self-assessors). In case this is true, we may use the sign of the slope of the regression between contest duration and winner RHP for each focal individual to determine if the individual adopt a mutual (negative slope) or self (positive slope) assessment strategy. However, individuals performing self-assessment may also show negative slopes (although with small absolute values) due to random variation in fight duration among contests. Therefore, before assigning the assessment strategy of each individual, it is necessary to test whether there is an indication of a mixed population. For this, we propose the usage of tests that compare the expected proportion of negative and positive slopes in a given sample considering that the population is entirely composed of mutual or self-assessors against the observed proportion in the sample. Both chi-square and binomial tests are suitable for this purpose. However, since this approach has never used before, Paulo Piexoto (Universidade Federal de Minas Gerais) and I developed an individual based simulation model to test the efficacy of these tests in indicating whether a population deviates from the two expected extremes (all individuals performing mutual assessment or all individuals performing self-assessment). This model was based on the framework proposed by Chapin et al. (2019), but with the modifications described below.

First, three groups containing 100 individuals each were created. Each individual has a RHP value that was randomly drawn from a normal distribution with a mean of 50 and a standard deviation of 10. After this, the individuals were randomly separated into groups of three individuals. In each triad, the individual with the smallest RHP value was designated to be the focal individual and was paired to fight a dyadic contest against each rival in the group. Since the focal individual always had the smallest RHP value in each triad, it was assigned to be the loser in both contests. Therefore, the duration of the contest was determined according to the assessment strategy adopted by the focal individual. If the focal individual adopted a mutual-assessment strategy, the duration of the contest would be inversely related with the RHP difference between the focal individual and his opponent (equation 1). If the focal individual adopted a self-assessment strategy, the duration of the contest was positively associated with the RHP value of the focal individual (equation 2). To obtain the contest duration for each fight, the contest durations of all interactions were calculated, assuming that all focal individuals adopted a mutual assessment strategy. Then a second group of contest durations were calculated, assuming that all focal individuals adopted a self-assessment strategy. After this, the assessment strategy that should be adopted by each individual was randomly determined and the corresponding contest duration chosen. In each simulation, the proportion of mutual to self-assessors was changed from 100/0 to 0/100 in steps of 10. For each proportion, the simulation was repeated 1000 times.

Equation 1: Contest duration value for fights in which the focal individual adopted a mutual assessment strategy. The variation value was randomly drawn from normal distribution with mean 0 and standard deviation 5.

$$\text{Contest duration}_{(\text{mutual assessor})} = \text{Max}(\text{RHP}_{\text{loser population}}) + (\text{RHP}_{\text{focal loser}} - \text{RHP}_{\text{rival winner}}) + \text{Variation}$$

Equation 2 – Contest duration value for fights in which the focal individual adopted a self-assessment strategy. The variation value was randomly drawn from normal distribution with mean 0 and standard deviation equal to the standard deviation obtained for contest durations in equation 1.

$$\text{Contest duration}_{(\text{self-assessor})} = \text{Min}(\text{RHP}_{\text{loser population}}) + \text{RHP}_{\text{focal loser}} + \text{Variation}$$

After determining the contest duration that should be used for each focal loser in each contest, the slope of an ordinary least squares (OLS) linear regression was calculated, with the contest duration as the response variable and the RHP of each opponent in a triad as the predictor variable. This was performed separately for each focal individual. Although the slope estimation using an OLS linear regression is trivial when the focal individual must fight against two rivals (generating just two values to perform the estimation), we opted to maintain this estimation because it is the recommended approach when the focal individual must fight against more than two rivals. This procedure produced 100 slopes in each simulation. It is important to note that, while all individuals performing mutual assessment are expected to show negative slopes, half of the individuals performing self-assessment are also expected to show a negative slope. This is expected because the contest duration exhibited by the focal individual under self-assessment should be similar among different fights, but with a small amount of random variation. Therefore, while a population entirely composed of mutual assessors should provide 100% of negative slopes, a population composed of 100 self-assessors should exhibit 50% of negative slopes. In the same way, a population composed of 50% mutual/self-assessors should show 75% of individuals with negative slopes (Table 6). Therefore, the raw proportion of negative slopes in a population provides an indication of the true proportion of mutual to self-assessors. However, to formally test when a population is composed of mutual and self-assessors using an inferential test, we evaluated two approaches. The first one is the use of a Chi-square test and the second one the use of a binomial test. For both analyses, we propose to test whether there was indication of a deviation from 99/1 mutual/self-assessors whenever the observed proportion of negative slopes vary between 75% and 100% and from 50/50 mutual/self-assessors when the observed proportion of negative slopes vary between 50% and 74%. To investigate the efficiency of each test in indicating whether the population deviated from a single assessment strategy, we quantified the number of times that each test provided a significant result among the 1000 simulations for each proportion of mutual to self-assessors.

iv. Assessment strategy identification: Chapin et al., framework

To determine which assessment strategy each focal cricket used and to assess whether there is individual variation in assessment strategy use, a linear model of total duration and winner body weight was fitted for each focal and its opponents using the *MASS* package and

'lm' function (Veneables & Ripley, 2002). Only fights where the focal individual lost were included, and only focal individuals that lost at least twice were included. This resulted in the exclusion of three focal individuals from the analysis (n focal crickets included= 27, n fights included= 104). The slope of the linear regression was used to determine the assessment strategy being used by each individual. As indicated by the simulation, the prediction for a population made up of entirely mutual assessors would be that 100% of the slopes are negative, while the prediction for a population of entirely self-assessors is that 50% of the slopes are negative due to random variation. Therefore, a percentage of 55-95% of negative slopes would indicate a mixed population and that individual variation is occurring.

v. Do crickets switch assessment strategy between contest phases?

Taylor and Elwood framework: To determine the assessment strategy used in each phase, I repeated the process for identifying the assessment strategy used, but instead of using total contest duration in the LMMs, I used the duration of phase 1 and phase 2 separately (Hsu et al., 2008; Lobregat et al., 2019). Again, separate models were made for winners and losers and likelihood ratio tests were performed. Fights that didn't escalate were excluded from the phase 2 model (n fights included= 131).

Chapin et al., framework: The methodology for identifying which assessment strategy each focal cricket used was repeated (i.e., separate slopes for each focal individual were calculated) but instead of using total contest duration a linear model was fitted for each phase using the duration of that phase. Fights that didn't escalate were excluded from the phase 2 model (n focal crickets included= 25, n fights included=98).

vi. Effect of personality

To determine whether personality explains between-individual variation in the assessment strategy used by *T. commodus*, the repeatability of the responses in the personality assays were first assessed. To do this I fitted a univariate linear mixed model for each behaviour and calculated the repeatability of each behaviour using *lme4* (Bates et al., 2015), *lmttest* (Zeileis & Hothorn, 2002) and *tidyverse* (Wickham et al., 2019) packages with 'lmer', 'lmttest' and 'tidy' functions. In the univariate model age, test number and body weight were included as fixed effects and cricket ID was included as a random effect. The repeatability was calculated as between-ID variance divided by the sum of between-ID variance and

residual variance (Nakagawa & Schielzeth, 2010). Once the most repeatable behaviour was identified, it was averaged across the three tests. A linear regression model, using package *MASS* and function 'lm' (Veneables & Ripley, 2002), was then fitted with the slopes of the focal individual's fights from the previous analysis as the response variable and the average behavioural response (i.e. time taken for body to emerge) as the explanatory fixed variable.

Results

Traits associated with fighting ability

The AICc scores for each of the body traits were almost identical (Table 5), suggesting that all the traits measured are equally useful as proxies for RHP. However, since bodyweight had a slightly lower AICc score, I will use this as a proxy for RHP in all subsequent analyses.

Table 5: AICc scores for each model comparing body traits against the probability of winning the contest.

	AICc Score	Delta AICc
<i>Body weight</i>	60.495	0
<i>Body length</i>	60.627	0.132
<i>Pronotum width</i>	60.903	0.408
<i>Hind femur length</i>	60.985	0.49

Assessment strategy identification: Taylor and Elwood framework

There was a positive but not significant relationship between contest duration and loser body weight ($\beta = 40.996$, $SE = 27.431$, $\chi^2 = 2.0215$ and $p = 0.1551$, Figure 5A). The relationship between contest duration and winner body weight was also not significant ($\beta = -1.726$, $SE = 25.465$, $\chi^2 = 0.0021$ and $p = 0.9632$, Figure 5B). The insignificant relationship of loser body weight and contest duration does not align with the predications of either self or mutual assessment.

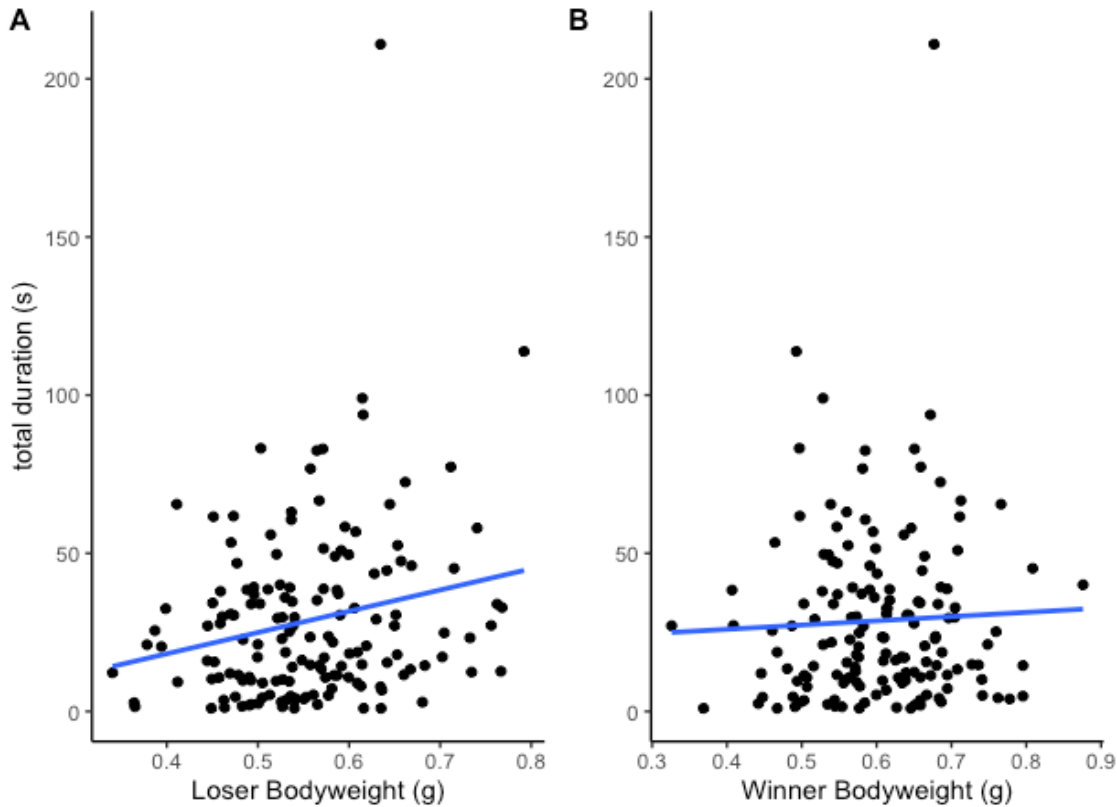


Figure 5: Relationship between overall contest duration and (A) body weight of losers and (B) bodyweight of winners in *Teleogryllus commodus* contests.

Simulation model for assessment strategy identification

For each proportion of mutual to self-assessors investigated, we obtained proportions of negative slopes similar to the theoretical expectations (Table 6). In fact, the median proportion of negative slopes increased from 50% when all individuals were assigned to perform self-assessment to 100% when all individuals were assigned to perform mutual assessment (Figure 6). This pattern was unaffected when we changed the variations used in equations 1 and 2 to calculate the contest time for each focal individual.

When the population had more than 50% of mutual assessors, the efficiency of both the chi-square and the binomial tests in detecting the existence of mixed strategies in the population were high, even when the population was near to a single strategy (i.e., 90% of mutual assessors, Table 6). In fact, for proportions of mutual to self-assessors between 80/20 and 50/50, both tests never indicated that the population was entirely composed of mutual assessors. However, when the population consisted of 90% of individuals performing self-assessment, both tests had a low efficiency in detecting deviations from a single strategy. The

efficiency rose to more than 80% (with major increases for the binomial test) when the proportion of self-assessors reached 70% of the population. Therefore, for sample sizes of 100 triads, both tests seem to provide a reliable way to evaluate whether there is evidence of mixed strategies in a population for most of the possible combinations of mutual and self-assessors.

Table 6: Summary results for simulations involving different numbers of mutual and self-assessors in a population of 100 focal individuals (1000 simulation for each combination). The number of mutual/self-assessors indicate how many focal individuals were designed to adopt each assessment strategy in the population in each simulation. The expected percentage of negative slopes indicate how many negative slopes should be estimated in linear regressions between fight duration of a focal individual and the RHP value of its opponents (two contest duration values for each focal individual). The percentage of correct support for mutual assessment in the binomial / chi-square tests indicate the percentage of significant results of binomial and chi-square tests used to test whether the proportion of negative slopes deviated from the expected values when the population is entirely composed of mutual assessors (used when the observed proportion of negative slopes varied between 75% and 100%) or entirely composed of self-assessors (used when the observed proportion of negative slopes varied between 50% and 54%). Tests were not run when 100% or 50% of slopes were negative since these were the expected values when the population consisted of a single assessment strategy.

Number of mutual/self- assessors	Expected percentage of negative slopes	Percentage of correct support for mutual assessment in the binomial / chi-square tests	Percentage of correct support for self-assessment in the binomial / chi-square tests
100/0	100	-	
90/10	95	92 / 97.1	
80/20	90	100	
70/30	85	100	
60/40	80	100	

50/50	75	100	98.9/98.5
40/60	70		96.2/94.8
30/70	65		88.3/83.5
20/80	60		57/48.9
10/90	55		21.1/15.6
0/100	50		-

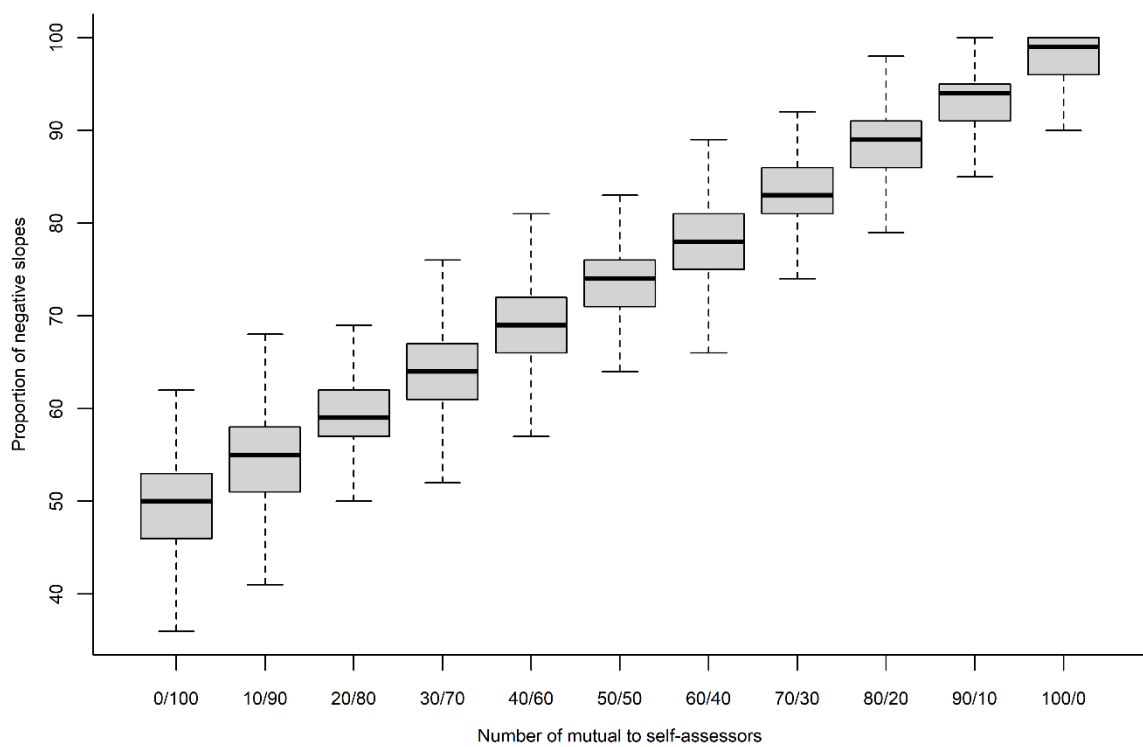


Figure 6: Median value of the proportion of negative slopes obtained in each simulation in relation to the number of mutual to self-assessors. Each simulation produced 100 slopes estimated from linear regressions between fight duration of a focal individual and

Assessment strategy identification: Chapin et al., framework

Focal individuals did not always lose every one of their 5 fights despite having a lower bodyweight; to be included in the analysis each individual had to lose at least two of their fights. This meant that from the original 31 focal crickets tested, 27 were included in the analysis, with the number of fights ranging from 2-5. 59% (16/27) of slopes were negative (Figure 7).

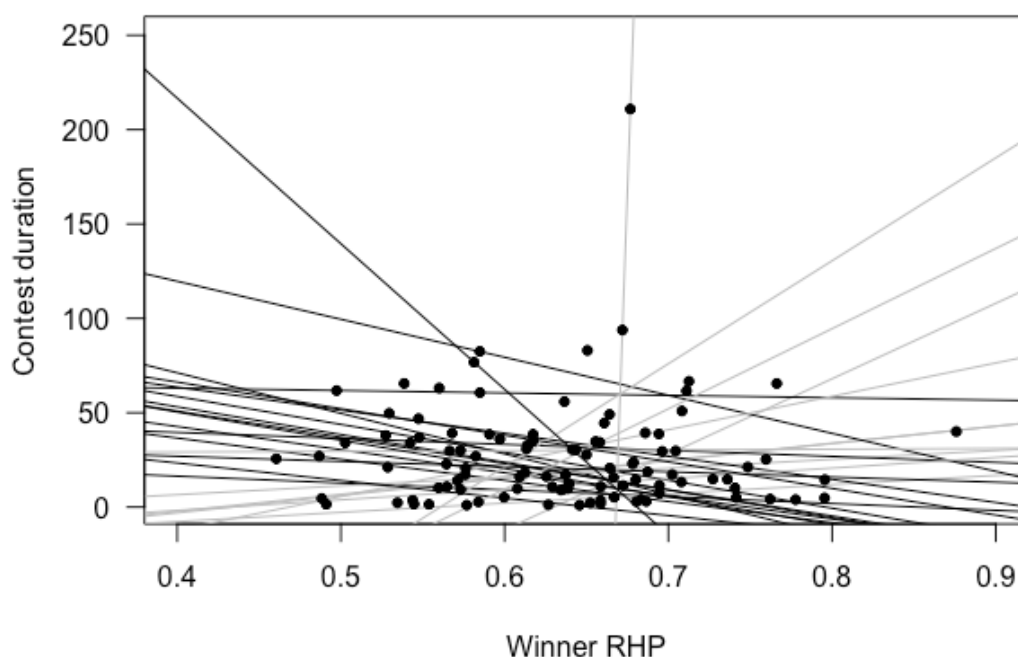


Figure 7: Relationship between overall contest duration and bodyweight of winners for each focal individual ($n=27$) in *Teleogryllus commodus* contests. Black lines indicate slopes < 0 and grey lines indicate slopes ≥ 0 .

Is switching of assessment strategy occurring?

i. Taylor and Elwood framework:

There was no significant relationship between phase 1 duration and loser body weight ($\beta=1.048$, $SE=1.739$, $\chi^2=1.287$ and $p=0.864$, Figure 8A). The relationship between phase 1 and winner bodyweight was also not significant ($\beta=2.459$, $SE=1.727$, $\chi^2=3.938$ and $p=0.415$, Figure 8B). For phase 2, there was a significant positive relationship between phase 2 duration and loser body weight ($\beta=48.88$, $SE=32.24$, $\chi^2=6.931$ and $p=0.0313$, Figure 8C), the

relationship between phase 2 and winner body weight was also negative but non-significant ($\beta=-16.92$, $df=127.94$, $SE=27.12$, $\chi^2= 0.290$ and $p=0.865$, Figure 8D).

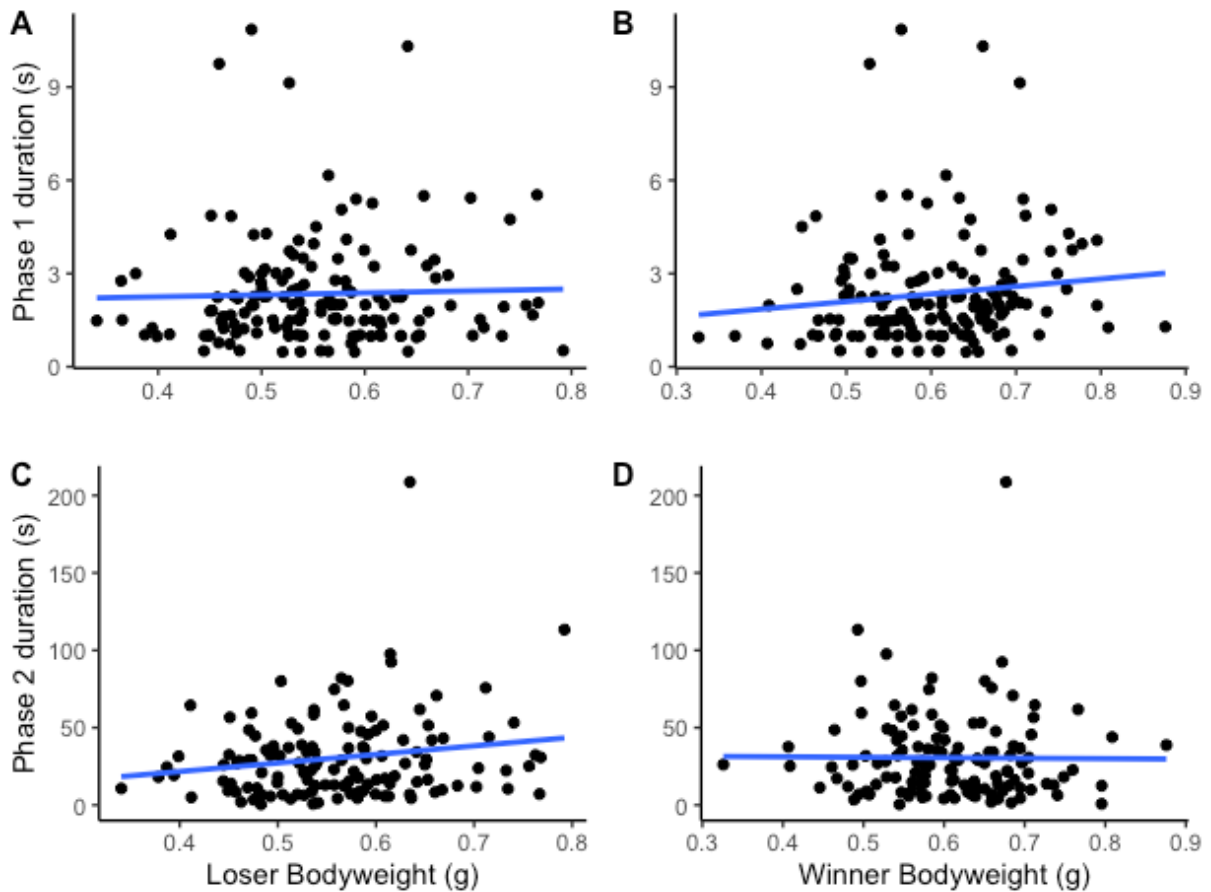


Figure 8: Relationship between phase 1 contest duration and (A) body weight of losers and (B) bodyweight of winners. Relationship between phase 2 contest duration and (C) body weight of losers and (D) bodyweight of winners in *Teleogryllus commodus* contests.

ii. Chapin et al., framework

For phase 1, 48% (13/27) of slopes were negative (Figure 9). Two focal individuals were excluded from phase 2 analysis as they did not lose any fights which escalated. 60% (15/25) of slopes for phase 2 were negative (Figure 9).

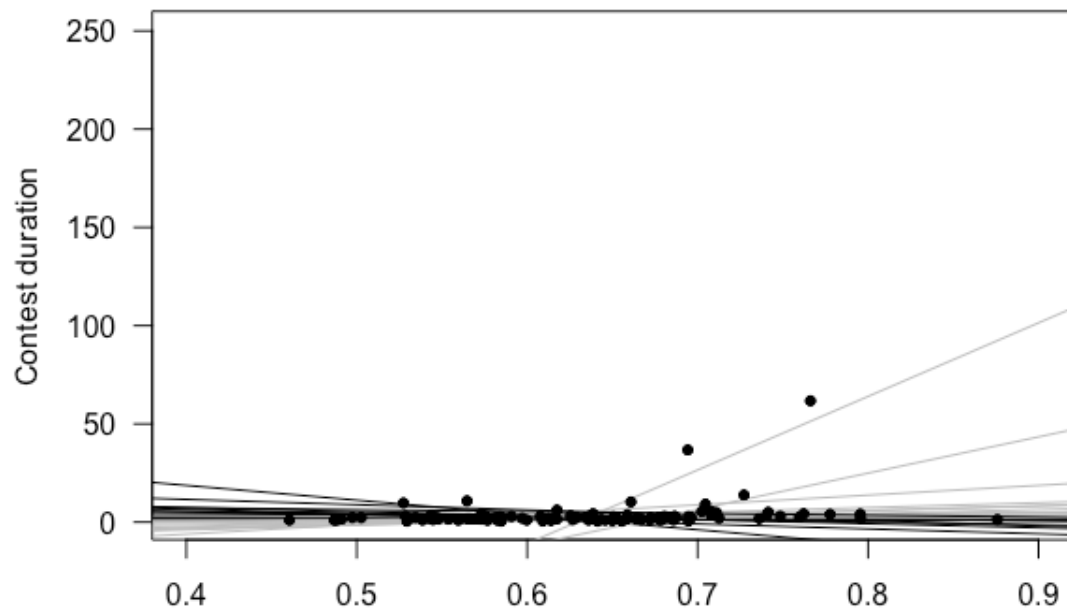
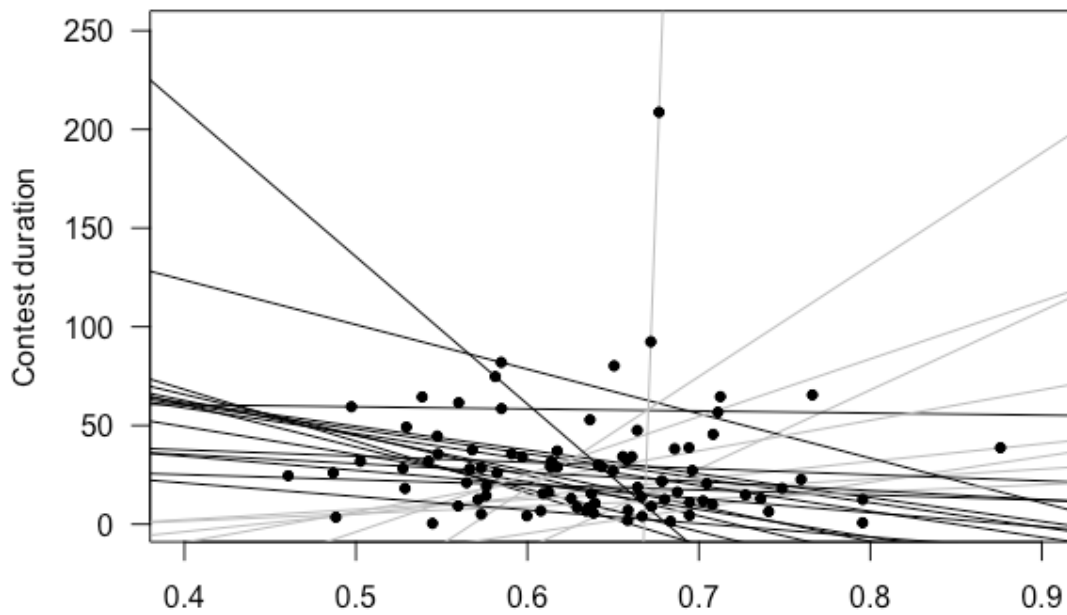
A**B**

Figure 9: Relationship between bodyweight of winners and (A) phase 1 contest duration and (B) phase 2 contest duration for each focal individual in *Teleogryllus commodus* contests. Black lines indicate slopes < 0 and grey lines indicate slopes ≥ 0 .

Inter-individual variation and repeatability

i. Effect of age, test number and weight

Age did not have a significant effect on the repeatability of the latency for the body to emerge ($p = 0.377$) or on latency for the cricket to touch the leaf ($p = 0.563$). Test number also did not have a significant effect on the repeatability of either behaviours ($p = 0.843$ and 0.347 respectively). Likewise, the effect of weight was also insignificant ($p = 0.875$ and 0.910 respectively).

ii. Effect of ID

Cricket ID had a significant effect on both latency for the body to emerge ($p < 0.0001$) and latency to touch the leaf ($p = 0.0002$).

iii. Repeatability of behavioural responses

Both behavioural responses (latency for head to emerge, time taken to touch the leaf) were repeatable between assays, with latency for the body to emerge having a higher repeatability score of 0.504 (95% CI: $0.368-0.589$) than latency to touch the leaf (repeatability: 0.398 [95% CI: $0.499-0.673$]). Therefore, latency for the body to emerge was used for further analysis.

Effect of Inter-individual variation on assessment strategy used

There was no significant correlation between latency for the body to emerge (boldness) and the slope of the relationship between winner RHP and contest duration ($\beta = -0.957$, $df = 25$, $SE = 4.611$, $R^2 = 0.0017$, $p = 0.837$) (Figure 10). I also ran the analysis with an outlier removed where the contest duration was magnitudes higher than the other contests, but this did not change the outcome of the results ($\beta = 0.0033$, $df = 24$, $SE = 0.2449$, $R^2 = >0.0001$, $p = 0.9893$).

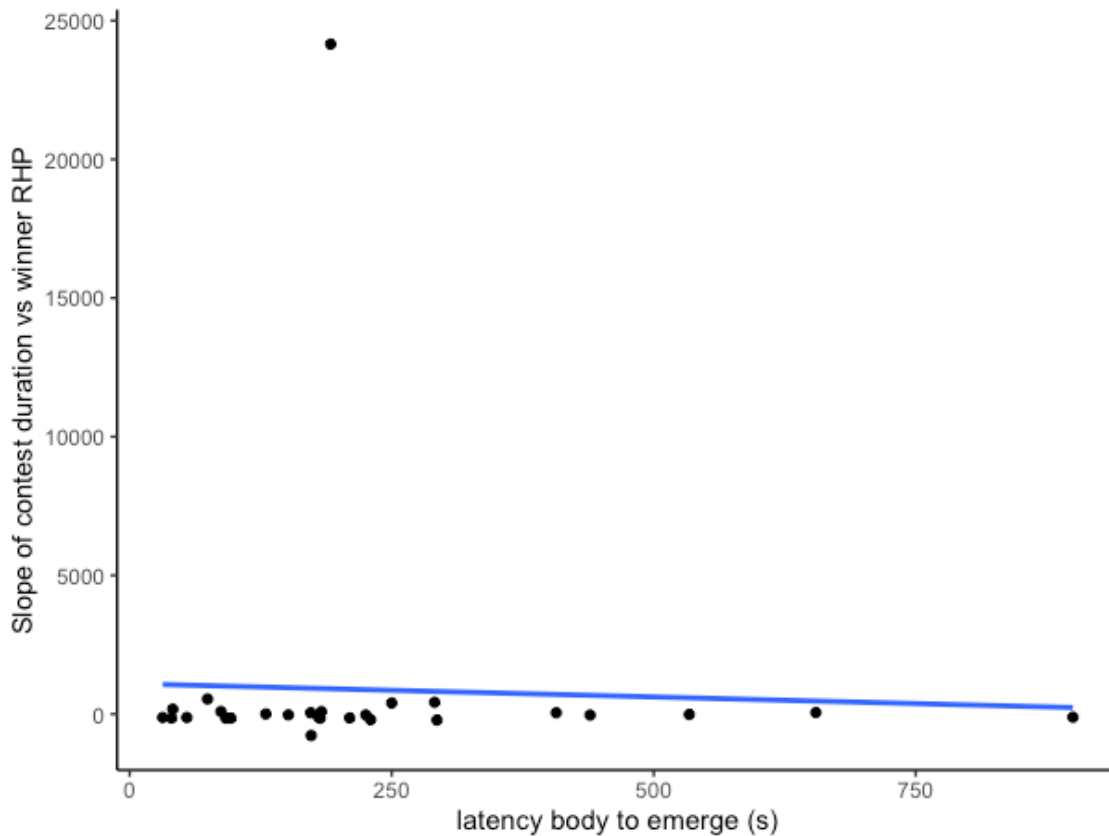


Figure 10: Relationship between boldness (latency for body to emerge in a novel environment) and assessment strategy (slope of the relationship between overall contest duration and winner RHP) in *Teleogryllus commodus*.

Discussion

This chapter investigated whether there was evidence for variation in the assessment strategy employed by *Teleogryllus commodus* at both the population and individual level. While the findings from the currently used analysis framework (Taylor and Elwood, 2003) were inconclusive, the newly proposed framework (Chapin et al., 2019) showed that there was population-level variation in the use of assessment strategies, with a mixture of 20% of individuals using the CAM or SAM models and 80% of individuals using (E)WOA. The Chapin et al., (2019) analysis also indicated that there is evidence for within-individual variation (i.e., switching between phases) in the use of assessment strategies. This chapter also investigated whether the variation in assessment strategies used among individuals was explained by personality, but there was no significant relationship between an individual's

boldness and the slope of the relationship between contest duration and winner RHP. As the first empirical application of the Chapin et al., (2019) methodology, these results show the improvements that this methodology can make to our understanding of animal contests, as it is able to consider individual variation in assessment strategy use as well as indicating whether switching of assessment strategies is occurring between phases of conflict.

*Assessment strategy used by *Teleogryllus commodus**

The results of the analysis using the Taylor and Elwood (2003) framework were inconclusive as none of predictions from any of the models were met. These inconclusive results may be due to the framework only determining the assessment strategy use at the population level rather than at the individual level. Identifying variation among individuals requires repeated testing of the same individuals using the more recently proposed analysis framework from Chapin et al., (2019), which assesses individuals separately to gain a better picture of what is occurring in the population. Although a negative slope describing the relationship between winner RHP and contest duration indicates that the CAM (self-assessment) or SAM (mutual assessment) models are being used, 50% of individuals using (E)WOA (self-assessment) are also expected to show a negative slope. Therefore, if 100% of the population are using (E)WOA, we would expect $\geq 50\%$ of the slopes to be negative, while if the population consists of 100% CAM/SAM, we expect 100% of the slopes to be negative. If individual variation in the use of mutual or self-assessment is occurring, then we would expect the population to be mixed and would expect 55-95% of slopes to be negative depending on the ratio of (E)WOA: CAM/SAM. Here I tested and confirmed these expectations using the simulation presented here. Since 59% of the slopes of winners RHP against total contest duration were negative, this population of *T. commodus* is comprised of a mix of individuals using E(WOA) and CAM or SAM. In order to determine if those 20% with negative slopes are using self-assessment (CAM) or mutual assessment (SAM) further analysis is required. It should also be noted that at a 20/80 mix of assessment strategies, the framework is only ~50-60% accurate at determining the proportions of the models being used, as indicated by the results of the simulation. Therefore, the mix may not be exactly 20:80% (E)WOA to SAM/CAM, and care should be taken when applying these results.

Unlike other studies which found clear evidence for either self-assessment or mutual assessment (Benítez et al., 2017; Bridge et al., 2000; Moore et al., 2008; Painting & Holwell, 2014; Prenter et al., 2006; Schnell et al., 2015; Sun et al., 2019; Taylor et al., 2001; Tedore & Johnsen, 2015) the analysis using the Taylor and Elwood (2003) framework was unable to clearly determine the assessment strategy that my population of *Teleogryllus commodus* uses. However, many other studies have also not been able to conclusively identify the assessment strategy used and instead found evidence for more than one model or no support for any models (Briffa, 2008; Glass & Huntingford, 1988; Jennings et al., 2004; Kelly, 2006; McCambridge et al., 2022; Peixoto & Benson, 2012; Stuart-Fox & Johnston, 2005). For example, an assessment of Wellington tree weta (*Hemideina crassidens*) found a positive correlation between loser size and contest duration but a negative (non-significant) correlation between winner size and contest duration (Kelly, 2006). Their results suggest self-assessment is the best model but due to the negative relationship between winner size and contest duration the results are inconclusive. Similarly, a study of fallow deer (*Dama dama*) contests did not find any evidence supporting the main predictions of either self or mutual assessment (Jennings et al., 2004). My results demonstrate why improvements on the Taylor and Elwood (2003) analysis may need to be made for studies that have had mixed or inconclusive results. The Chapin et al., (2019) analysis was able to provide greater insight into the assessment strategy used by *T. commodus* and showed that the inconclusive results may have been due to population being comprised of a mix of assessment strategies.

Switching of assessment strategy between phases of contest

Assessing each phase of the contest individually using the Taylor and Elwood (2003) framework provided inconclusive evidence for whether switching occurred between contest phases. As phase 1 results did not align with the predictions of either the self-assessment models or the mutual assessment model predictions. Phase 2 results, however did align with predictions of the (E)WOA model. Using the Chapin et al., (2019) analysis I was able to investigate each phase more closely. Analysing each phase separately using this framework showed that for phase 1 $\geq 50\%$ of the slopes describing the relationship between winner RHP and phase duration are negative indicating that all individuals were using (E)WOA. In phase 2, 60% of the slopes were negative, suggesting that $\sim 20\%$ of the individuals in the population were using CAM or SAM assessment model rather than the (E)WOA model,

following a similar pattern to when both phases of the contest were analysed together. This finding is similar to the other studies that have assessed the phases of contest separately and found that assessment strategy switching is occurring in neotropical crickets (*Melanotes ornata*) (Lobregat et al., 2019) and killifish (*Kryptolebias marmoratus*) (Hsu et al., 2008) where both species switch from using mutual assessment in the initial phase to self-assessment when the contest escalates. However, my results do not necessarily mean switching is occurring as phase 1 may not be included in the contest. Since analysis of phase 1 using the Taylor and Elwood (2003) did not meet the predictions of self-assessment or mutual assessment models, and the repeated contest approach of the Chapin et al., (2019) methodology always assigns an assessment strategy even if the behaviour doesn't involve a fight, this suggests that phase 1 may not have involved contest behaviour. Rather, it may be a quasi-agnostic behaviour where the individuals are performing prior evaluation to determine if the opponent is a rival and have not yet committed to a contest (Pinto & Peixoto, 2019). Therefore, phase 1 results may not be sufficient to truly assess whether switching is occurring. Therefore, the contest elements within phase 2 may need to be separated out into further stages and assessed separately.

Switching may also be easier to detect in species that have more distinct phases during conflict, or in species with greater size disparities between males where accurate information is easy to gain during an initial mutual assessment phase (Faber & Baylis, 1993). For example, the New Zealand giraffe weevil (*Lasiornychus barbicornis*), in which males show extreme size variation (Painting et al., 2014), have been found to most likely employ mutual assessment during contests (Painting & Holwell, 2014). However, separate analyses of each phase may show that when contests escalate the giraffe weevils switch to self-assessment.

Finally, a switch in assessment strategies may be more likely to occur in conflict that escalated between a resident male and an intruder (Peixoto & Benson, 2012), since all crickets in my experiments were placed into a novel environment for the contest and allowed equal acclimation time in the testing arena, resident/intruder effects would be minimal. Further study would be required to determine if switching is more common when resident/intruder effects are stronger. Therefore, as more studies begin to separate out the

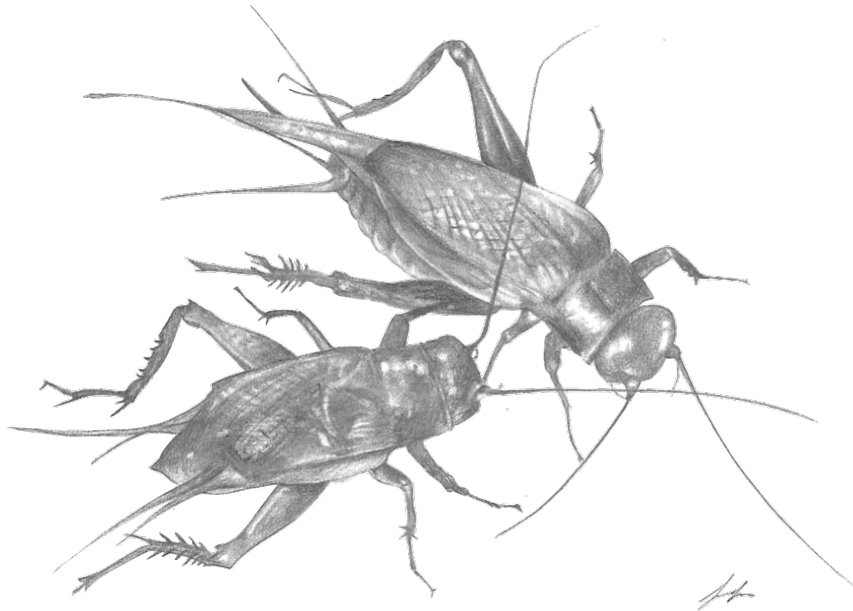
phases and analyse them individually, there may be growing evidence that other species also switch assessment strategies as contests escalate.

Personality as an explanation of variation in assessment strategy use

Boldness was not significantly related to the slope of the relationship between winner RHP and contest duration for the repeated focal male trials, in this population of *T. commodus*. I also did not find evidence for a behavioural syndrome linking boldness and aggression, an important behaviour involved in conflict (Chapter 2). However as discussed in Chapter 2, this may be due to the effects of domestication, as this population of *T. commodus* has been commercially bred in captivity, fed ad libitum and exposed to a predator-free environment for many generations, which likely means that this population has experienced very different inbreeding, natural, sexual and artificial selection pressures than wild populations of *T. commodus* (Wilson et al., 2010). Therefore, future studies using a wild population or species with previously identified boldness-aggression behavioural syndromes may find differing results. Similarly, studies with species that show individual variation in assessment strategy may also find a link between personality and assessment strategy use. Therefore, while I did not find any link between personality and assessment strategies, it may still be a possible explanation for previously inconclusive results when applying game theory to animal contests.

Chapter four

General Discussion



This thesis aimed to provide explanations for why previous studies have found mixed or inconclusive results when applying evolutionary game theory to animal contests. Individual variation in assessment strategy use, the effect of personality, switching of assessment strategies, and inappropriate statistical analyses were identified as possible explanations. Here I will discuss the plausibility of these factors as possible explanations as well as the limitations of my work and where I believe future work should focus.

Individual variation in assessment strategy use

While the Taylor and Elwood (2003) analysis framework has significantly progressed our understanding of contest dynamics, it is limited to determining assessment strategies at the species/population level and is therefore unable to detect individual variation. As the first study to apply the Chapin et al., (2019) methodology to empirical data, my results clearly demonstrate the advantages of using focal individuals with repeated contests, which allows us to determine the assessment strategy used at both the individual level and the species/population level. While the more commonly used Taylor and Elwood (2003) analysis was unable to clearly determine the assessment strategy use in *Teleogryllus commodus*, the Chapin et al., (2019) analysis was able to determine that my population of *T. commodus* uses a mix of assessment strategies (Chapter 3). These results show how crucial improvement of the analysis frameworks, like the Chapin et al., (2019) methodology, could be for assessing species that have individual variation where the population is made up of a mix of the two assessment strategy classifications. I would suggest that previous studies may have been limited in determining the assessment strategies at the population level without considering possible between-individual variation in strategy use which led to inconclusive or mixed results. Therefore, individual variation is a plausible explanation for previous inconclusive results when applying game theory to animal contests.

Personality as an explanation for individual variation in assessment strategies

To assess the effect of personality on assessment strategy use and contest dynamics I first had to determine whether *Teleogryllus commodus* had personality (consistent individual variation in behavioural responses). I did indeed find that individual *T. commodus* crickets

repeatedly varied in their general activity in their home environment, their boldness in a novel environment and towards a novel object, and their aggression towards conspecifics, but not in their boldness after a predation risk event (Chapter 2). I then assessed whether there was a behavioural syndrome linking these behavioural traits to see if boldness might affect contest dynamics via underlying mechanisms also affecting aggression. However, I found no correlation between boldness, activity, or aggression, thus suggesting that personality might not influence *T. commodus* contest behaviour (Chapter 2). I still went on to determine whether there was a relationship between boldness and the slope of the winner RHPs against contest duration (indicative of the assessment strategy being used) to investigate whether boldness might have an effect. However, there was no significant relationship between these factors (Chapter 3). Therefore, personality does not appear to have any effect on contest dynamics in *T. commodus*. However, the lack of repeatability of individual variation in boldness after a predation risk event suggests that this population of *T. commodus* may have been subject to domestication selective pressures, and may have developed different behaviours to a wild population (Wilson et al., 2010). Perceived predation risk has been shown to induce a behavioural syndrome between boldness and aggression, therefore the results may have been different with a wild-type population (Bell & Sih, 2007). I also only assessed boldness, but other behaviours may also affect contest behaviour via a behavioural syndrome. Personality may also have a stronger effect on species that do show individual variation in assessment strategy use, therefore I cannot rule out personality as a confounding effect on studies applying game theory to animal contests just yet.

Assessment strategy switching between contest phases

Similarly to individual variation, assessment of the separated phases of conflict suggested that switching of assessment strategies between phases may be possible (Chapter 3). However, again only the Chapin et al., (2019) was able to clearly show this, demonstrating the advantage of using this method. Using the Taylor and Elwood (2003) framework provided inconclusive results which did not align with the predictions from any of the assessment strategy models (Chapter 3). Although my results could not conclusively determine that switching is occurring in my study species, other studies have found evidence of switching (Hsu et al., 2008; Lobregat et al., 2019). Therefore, I would not rule

out switching as a possible explanation for previously inconsistent results in other species. However, I suggest that switching may be more applicable to species with a greater distinction between phases of conflict, greater body or weapon size disparities and/or stronger resident vs intruder effects where an initial phase of mutual assessment may be more prevalent (Faber & Baylis, 1993; Peixoto & Benson, 2012). Therefore, analysing phases of conflict separately is important when determining the assessment strategies used during animal conflicts and switching of assessment strategies remains a plausible explanation for mixed or inconclusive results in previous studies.

Limitations and future directions

I believe the main limitation of the research in this thesis is the use of only one species. Were I to do this again, I would assess more than one species and in particular I would use species that had previously been assessed but found inconclusive results, such as the Wellington tree weta (Kelly, 2006), to more easily determine which, if any, of my chosen factors caused these inconclusive results. While my research has shown how important the Chapin et al., (2019) methodology may be for applying game theory to animal contests, it needs to be applied to other species, especially those that may have individual variation in assessment strategy use and have a mixed population. Also had time allowed, I would have liked to assess other behaviours in Chapter 2 in addition to activity, boldness (novel environment and anti-predation context) and aggression to determine if there was a behavioural syndrome at all in *T. commodus*. In particular, I would investigate whether any behaviours are linked to aggression and could potentially have an impact on contest dynamics. Similarly, based on my results from Chapter 2, I would have liked to repeat my experiments on a wild caught population to determine the effects of domestication on personality, and whether the assessment strategy used by the wild type *T. commodus* is the same as my commercially bred population. Additionally, the results of the simulation (Chapter 3) indicate a limitation in the Chapin et al., (2019) framework to be able to determine the proportion of self-assessors to mutual assessors, when the population is made up of nearly all mutual or self-assessors (i.e. at 90-80% self-assessment or 90% mutual assessment). This means that the results of the analysis may indicate that a population is entirely made up of one assessment type, however, ~10% of the population may be using a different assessment strategy. Therefore, some consideration of this should be applied

when using the Chapin et al., (2019) methodology. Also, similarly to the Taylor and Elwood (2003), the Chapin et al., (2019) framework is unable to distinguish between the mutual assessment model SAM and the self-assessment model CAM, as both predict a negative relationship between winner RHP and contest duration. Therefore, if there is evidence for SAM/CAM further information is required to determine which assessment strategy is being used. Overall, I think my results highlight individual variation and switching of assessment strategies as well as the effects of personality as important areas for future research. However, not only these factors be considered, but so should age, environment, motivation and previous experience as these may also effect assessment strategy use (Briffa & Elwood, 2001; Chapin et al., 2019; Elwood et al., 2006; Hsu & Wolf, 1999).

Concluding remarks

The primary finding of this body of work, is that the Taylor and Elwood (2003) analysis framework, which has been most commonly used when determining assessment strategy use in species needs to be updated as it is insufficient to investigate variation in contest behaviour beyond the population level. I have demonstrated here that the Chapin et al., (2019) methodology provides some great advantages in this respect, but still needs to be tested with other species. Some evidence for switching of assessment strategies as contests escalate was provided, while effects of boldness/personality were not demonstrated in *Teleogryllus commodus*, but they both remain plausible reasons for previously inconclusive results. While I have shown that the analytic framework does need to be updated and switching and personality could be possible explanations for previous studies being unable to conclusively determine which assessment strategy a species uses, there may be a myriad of reasons and many factors that need to be considered when applying game theory to animal contests.

References:

- Alexander, R. D. (1961). Aggressiveness, Territoriality, and Sexual Behavior in Field Crickets (*Orthoptera: Gryllidae*). *Behaviour*, 17(2/3), 130–223.
- Andersson, M., & Iwasa, Y. (1996). Sexual Selection. *Trends in Ecology & Evolution*, 11(2), 53–58.
[https://doi.org/10.1016/0169-5347\(96\)81042-1](https://doi.org/10.1016/0169-5347(96)81042-1)
- Anestis, S. F. (2005). Behavioral Style, Dominance Rank, and Urinary Cortisol in Young Chimpanzees (*Pan troglodytes*). *Behaviour*, 142(9/10), 1245–1268.
- Archer, C. R., Zajitschek, F., Sakaluk, S. K., Royle, N. J., & Hunt, J. (2012). Sexual Selection Affects the Evolution of Lifespan and Ageing in the Decorated Cricket *Gryllodes Sigillatus*. *Evolution*, 66(10), 3088–3100. <https://doi.org/10.1111/j.1558-5646.2012.01673.x>
- Arnott, G., & Elwood, R. W. (2009). Assessment of Fighting Ability in Animal Contests. *Animal Behaviour*, 77(5), 991–1004. <https://doi.org/10.1016/j.anbehav.2009.02.010>
- Balsam, J. S., & Stevenson, P. A. (2021). Agonistic Experience during Development Establishes Inter-Individual Differences in Approach-Avoidance Behaviour of Crickets. *Scientific Reports*, 11(1), 16702. <https://doi.org/10.1038/s41598-021-96201-1>
- Balzarini, V., Taborsky, M., Wanner, S., Koch, F., & Frommen, J. G. (2014). Mirror, Mirror On The Wall: The Predictive Value of Mirror Tests for Measuring Aggression in Fish. *Behavioral Ecology and Sociobiology*, 68(5), 871–878. <https://doi.org/10.1007/s00265-014-1698-7>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1–48. <https://doi.org/10.18637/jss>.
- Bell, A. M. (2007). Future Directions in Behavioural Syndromes Research. *Proceedings of the Royal Society B: Biological Sciences*, 274(1611), 755–761. <https://doi.org/10.1098/rspb.2006.0199>

- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The Repeatability of Behaviour: A Meta-Analysis. *Animal Behaviour*, 77(4), 771–783. <https://doi.org/10.1016/j.anbehav.2008.12.022>
- Bell, A. M., & Sih, A. (2007). Exposure to Predation Generates Personality in Threespined Sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, 10(9), 828–834. <https://doi.org/10.1111/j.1461-0248.2007.01081.x>
- Benítez, M. E., Pappano, D. J., Beehner, J. C., & Bergman, T. J. (2017). Evidence for Mutual Assessment in a Wild Primate. *Scientific Reports*, 7(1), 2952. <https://doi.org/10.1038/s41598-017-02903-w>
- Bentsen, C. L., Hunt, J., Jennions, M. D., & Brooks, R. (2006). Complex Multivariate Sexual Selection on Male Acoustic Signaling in a Wild Population of *Teleogryllus commodus*. *The American Naturalist*, 167(4), E102–E116. <https://doi.org/10.1086/501376>
- Bonilla, M. L., Todd, C., Erlandson, M., & Andres, J. (2015). Combining RNA-seq and Proteomic Profiling to Identify Seminal Fluid Proteins in the Migratory Grasshopper *Melanoplus sanguinipes* (F). *BMC Genomics*, 16(1), 1096. <https://doi.org/10.1186/s12864-015-2327-1>
- Bridge, A. P., Elwood, R. W., & Dick, J. T. A. (2000). Imperfect Assessment and Limited Information Preclude Optimal Strategies in Male-Male Fights in the Orb-weaving Spider *Metellina mengei*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*. <https://doi.org/10.1098/rspb.2000.0997>
- Briffa, M. (2008). Decisions during fights in the house cricket, *Acheta domesticus*: Mutual or Self Assessment of Energy, Weapons and Size? *Animal Behaviour*, 75(3), 1053–1062. <https://doi.org/10.1016/j.anbehav.2007.08.016>
- Briffa, M., & Elwood, R. W. (2001). Motivational Change During Shell Fights in the Hermit Crab *Pagurus bernhardus*. *Animal Behaviour*, 62(3), 505–510. <https://doi.org/10.1006/anbe.2001.1764>

- Briffa, M., & Elwood, R. W. (2004). Use of Energy Reserves in Fighting Hermit Crabs. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1537), 373–379.
<https://doi.org/10.1098/rspb.2003.2633>
- Briffa, M., & Elwood, R. W. (2009). Difficulties Remain in Distinguishing Between Mutual and Self-Assessment in Animal Contests. *Animal Behaviour*, 77(3), 759–762.
<https://doi.org/10.1016/j.anbehav.2008.11.010>
- Briffa, M., & Lane, S. M. (2017). The role of Skill in Animal Contests: A Neglected Component of Fighting Ability. *Proceedings of the Royal Society B: Biological Sciences*, 284(1863), 20171596. <https://doi.org/10.1098/rspb.2017.1596>
- Briffa, M., Sneddon, L. U., & Wilson, A. J. (2015). Animal Personality as a Cause and Consequence of Contest Behaviour. *Biology Letters*, 11(3), 20141007.
<https://doi.org/10.1098/rsbl.2014.1007>
- Brown, W. D., Smith, A. T., Moskalik, B., & Gabriel, J. (2006). Aggressive Contests in House Crickets: Size, Motivation and the Information Content of Aggressive Songs. *Animal Behaviour*, 72(1), 225–233. <https://doi.org/10.1016/j.anbehav.2006.01.012>
- Bussiégre, L. F., Hunt, J., Jennions, M. D., & Brooks, R. (2006). Sexual Conflict and Cryptic Female Choice in the Black Field Cricket, *Teleogryllus Commodus*. *Evolution*, 60(4), 792–800.
<https://doi.org/10.1111/j.0014-3820.2006.tb01157.x>
- Camerlink, I., Turner, S. P., Farish, M., & Arnott, G. (2017). The Influence of Experience on Contest Assessment Strategies. *Scientific Reports*, 7(1), 14492. <https://doi.org/10.1038/s41598-017-15144-8>
- Campbell, D. J., & Shipp, E. (1979). Regulation of Spatial Pattern in Populations of the Field Cricket *Teleogryllus commodus* (Walker). *Zeitschrift Für Tierpsychologie*, 51(3), 260–268.
<https://doi.org/10.1111/j.1439-0310.1979.tb00688.x>

- Campbell, D. T., & Fiske, D. W. (1959). Convergent and Discriminant Validation by the Multitrait-multimethod Matrix. *Psychological Bulletin*, 56(2), 81–105.
<https://doi.org/10.1037/h0046016>
- Carere, C., Drent, P. J., Privitera, L., Koolhaas, J. M., & Groothuis, T. G. G. (2005). Personalities in Great Tits, *Parus major*: Stability and Consistency. *Animal Behaviour*, 70(4), 795–805.
<https://doi.org/10.1016/j.anbehav.2005.01.003>
- Carere, C., & Maestripieri, D. (2013). *Animal Personalities: Behavior, Physiology, and Evolution*. University of Chicago Press.
- Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlshaw, G., & Heinsohn, R. (2013). Animal Personality: What are Behavioural Ecologists Measuring? *Biological Reviews*, 88(2), 465–475. <https://doi.org/10.1111/brv.12007>
- Chang, C., Connahs, H., Tan, E. C. Y., Norma-Rashid, Y., Mrinalini, Li, D., & Chew, F. T. (2020). Female Spider Aggression is Associated with Genetic Underpinnings of the Nervous System and Immune Response to Pathogens. *Molecular Ecology*, 29(14), 2626–2638.
<https://doi.org/10.1111/mec.15502>
- Chang, C., Teo, H. Y., Norma-Rashid, Y., & Li, D. (2017). Predator Personality and Prey Behavioural Predictability Jointly Determine Foraging Performance. *Scientific Reports*, 7(1), 40734.
<https://doi.org/10.1038/srep40734>
- Chapin, K., James, Peixoto, P. E. C., & Briffa, M. (2019). Further mismeasures of animal contests: A new framework for assessment strategies. *Behavioral Ecology*, 30(5), 1177–1185.
<https://doi.org/10.1093/beheco/arz081>
- Chen, B., Liu, K., Zhou, L., Gomes-Silva, G., Sommer-Trembo, C., & Plath, M. (2018). Personality differentially affects individual mate choice decisions in female and male Western

mosquitofish (*Gambusia affinis*). *PLOS ONE*, 13(5), e0197197.

<https://doi.org/10.1371/journal.pone.0197197>

Chen, G., Vickery, V. R., & Kevan, D. K. (1967). A Morphological Comparison of Antipodean Teleogryllus Species. *Canadian Journal of Zoology* 45: 1215-1224 .

Clark, A. B., & Ehlinger, T. J. (1987). Pattern and Adaptation in Individual Behavioral Differences. In P. P. G. Bateson & P. H. Klopfer (Eds.), *Perspectives in Ethology: Volume 7 Alternatives* (pp. 1–47). Springer US. https://doi.org/10.1007/978-1-4613-1815-6_1

Coleman, K., & Wilson, D. S. (1998). Shyness and boldness in pumpkinseed sunfish: Individual differences are context-specific. *Animal Behaviour*, 56(4), 927–936.
<https://doi.org/10.1006/anbe.1998.0852>

Colléter, M., & Brown, C. (2011). Personality traits predict hierarchy rank in male rainbowfish social groups. *Animal Behaviour*, 81(6), 1231–1237.
<https://doi.org/10.1016/j.anbehav.2011.03.011>

Courtene-Jones, W., & Briffa, M. (2014). Boldness and asymmetric contests: Role- and outcome-dependent effects of fighting in hermit crabs. *Behavioral Ecology*, 25(5), 1073–1082.
<https://doi.org/10.1093/beheco/aru085>

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, 7(8), 734–739. <https://doi.org/10.1111/j.1461-0248.2004.00618.x>

Dammhahn, M., & Almeling, L. (2012). Is risk taking during foraging a personality trait? A field test for cross-context consistency in boldness. *Animal Behaviour*, 84(5), 1131–1139.
<https://doi.org/10.1016/j.anbehav.2012.08.014>

Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex*. John Murray.

- David, M., Auclair, Y., & Cézilly, F. (2011). Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context. *Animal Behaviour*, 81(1), 219–224.
<https://doi.org/10.1016/j.anbehav.2010.10.008>
- David, M., & Cézilly, F. (2011). Personality May Confound Common Measures of Mate-Choice. *PLOS ONE*, 6(9), e24778. <https://doi.org/10.1371/journal.pone.0024778>
- Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, 82(1), 39–54.
<https://doi.org/10.1111/1365-2656.12013>
- Dingemanse, N. J., & Réale, D. (2005). Natural Selection and Animal Personality. *Behaviour*, 142(9/10), 1159–1184.
- Dochtermann, N. A., & Jenkins, S. H. (2007). Behavioural syndromes in Merriam’s kangaroo rats (*Dipodomys merriami*): A test of competing hypotheses. *Proceedings of the Royal Society B: Biological Sciences*, 274(1623), 2343–2349. <https://doi.org/10.1098/rspb.2007.0622>
- Dochtermann, N. A., & Nelson, A. B. (2014). Multiple Facets of Exploratory Behavior in House Crickets (*Acheta domesticus*): Split Personalities or Simply Different Behaviors? *Ethology*, 120(11), 1110–1117. <https://doi.org/10.1111/eth.12284>
- Drinkwater, E., Robinson, E. J. H., & Hart, A. G. (2019). Keeping invertebrate research ethical in a landscape of shifting public opinion. *Methods in Ecology and Evolution*, 10(8), 1265–1273.
<https://doi.org/10.1111/2041-210X.13208>
- Duckworth, R. A. (2006). Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology*, 17(6), 1011–1019.
<https://doi.org/10.1093/beheco/arl035>

- Eccard, J. A., Liesenjohann, T., & Dammhahn, M. (2020). Among-individual differences in foraging modulate resource exploitation under perceived predation risk. *Oecologia*, 194(4), 621–634. <https://doi.org/10.1007/s00442-020-04773-y>
- Elwood, R. W., Pothanikat, R. M. E., & Briffa, M. (2006). Honest and dishonest displays, motivational state and subsequent decisions in hermit crab shell fights. *Animal Behaviour*, 72(4), 853–859. <https://doi.org/10.1016/j.anbehav.2006.01.025>
- Emlen, D. J. (2008). The Evolution of Animal Weapons. *Annual Review of Ecology, Evolution, and Systematics*, 39(1), 387–413. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173502>
- Enquist, M., & Leimar, O. (1982). Evolution of Fighting Behaviour: Decision Rules and Assessment of Relative Strength.
- Evans, A. R. (1983). A Study of the Behaviour of the Australian Field Cricket *Teleogryllus commodus* (Walker) (*Orthoptera: Gryllidae*) in the Field and in Habitat Simulations. *Zeitschrift Für Tierpsychologie*, 62(4), 269–290. <https://doi.org/10.1111/j.1439-0310.1983.tb02157.x>
- Faber, D. B., & Baylis, J. R. (1993). Effects of body size on agonistic encounters between male jumping spiders (*Araneae: Salticidae*). *Animal Behaviour*, 45(2), 289–299. <https://doi.org/10.1006/anbe.1993.1033>
- Favati, A., Leimar, O., & Løvlie, H. (2014). Personality Predicts Social Dominance in Male Domestic Fowl. *PLOS ONE*, 9(7), e103535. <https://doi.org/10.1371/journal.pone.0103535>
- Friard, O., & Gamba, M. (2016). *BORIS*: a free, versatile open-source event-logging software for video/audio coding and live observations.
- Ginsburg, B., & Allee, W. C. (n.d.). Some Effects of Conditioning on Social Dominance and Subordination in Inbred Strains of Mice. *PHYSIOLOGICAL ZOOLOGY*, 4, 22.

- Glass, C. W., & Huntingford, F. A. (1988). Initiation and Resolution of Fights between Swimming Crabs (*Liocarcinus depurator*). *Ethology*, 77(3), 237–249. <https://doi.org/10.1111/j.1439-0310.1988.tb00207.x>
- Gray, D. A., & Cade, W. H. (1999). Sex, death, and genetic variation: Natural and sexual selection on cricket song. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266(1420), 707–709. <https://doi.org/10.1098/rspb.1999.0693>
- Gruber, C. (2009). Behavioural variation in the field cricket (*Gryllus integer*), what is the role of heritable components? [Dipl, uni Wien]. <http://othes.univie.ac.at/7883/>
- Hack, M. A. (1997). The energetic costs of fighting in the house cricket, *Acheta domesticus* L. *Behavioral Ecology*, 8(1), 28–36. <https://doi.org/10.1093/beheco/8.1.28>
- Hadfield, J. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. *Journal of Statistical Software*, 33(2), 1–22.
- Hall, M. D., McLaren, L., Brooks, R. C., & Lailvaux, S. P. (2010). Interactions among performance capacities predict male combat outcomes in the field cricket. *Functional Ecology*, 24(1), 159–164. <https://doi.org/10.1111/j.1365-2435.2009.01611.x>
- Hardy, & Briffa. (2013). *Animal Contests*.
https://books.google.co.nz/books?hl=en&lr=&id=aQlCAQAAQBAJ&oi=fnd&pg=PR9&dq=Hardy+and+Briffa+2013&ots=97nf3jEfev&sig=NzMB_ZK6Kci-kzDFIkQHBZ4sFBs&redir_esc=y#v=onepage&q=Hardy%20and%20Briffa%202013&f=false
- Hedrick, A. V., & Kortet, R. (2012). Sex differences in the repeatability of boldness over metamorphosis. *Behavioral Ecology and Sociobiology*, 66(3), 407–412.
<https://doi.org/10.1007/s00265-011-1286-z>

- Hsu, Y., Earley, R. L., & Wolf, L. L. (2006). Modulation of aggressive behaviour by fighting experience: Mechanisms and contest outcomes. *Biological Reviews*, 81(1), 33–74.
<https://doi.org/10.1017/S146479310500686X>
- Hsu, Y., Lee, S.-P., Chen, M.-H., Yang, S.-Y., & Cheng, K.-C. (2008). Switching assessment strategy during a contest: Fighting in killifish *Kryptolebias marmoratus*. *Animal Behaviour*, 75(5), 1641–1649. <https://doi.org/10.1016/j.anbehav.2007.10.017>
- Hsu, Y., & Wolf, L. L. (1999). The winner and loser effect: Integrating multiple experiences. *Animal Behaviour*, 57(4), 903–910. <https://doi.org/10.1006/anbe.1998.1049>
- Hunt, J., Breuker, C. J., Sadowski, J. A., & Moore, A. J. (2009). Male–male competition, female mate choice and their interaction: Determining total sexual selection. *Journal of Evolutionary Biology*, 22(1), 13–26. <https://doi.org/10.1111/j.1420-9101.2008.01633.x>
- Jang, Y., Gerhardt, H. C., & Choe, J. C. (2008). A comparative study of aggressiveness in eastern North American field cricket species (genus *Gryllus*). *Behavioral Ecology and Sociobiology*, 62(9), 1397–1407. <https://doi.org/10.1007/s00265-008-0568-6>
- Jennings, D. J., Gammell, M. P., Carlin, C. M., & Hayden, T. J. (2004). Effect of body weight, antler length, resource value and experience on fight duration and intensity in fallow deer. *Animal Behaviour*, 68(1), 213–221. <https://doi.org/10.1016/j.anbehav.2003.11.005>
- Johnson, J. C., & Sih, A. (2005). Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): A role for behavioral syndromes. *Behavioral Ecology and Sociobiology*, 58(4), 390–396. <https://doi.org/10.1007/s00265-005-0943-5>
- Kar, F., Whiting, M. J., & Noble, D. W. A. (2016). Influence of prior contest experience and level of escalation on contest outcome. *Behavioral Ecology and Sociobiology*, 70(10), 1679–1687.
<https://doi.org/10.1007/s00265-016-2173-4>

- Kelly, C. D. (2006). Fighting for harems: Assessment strategies during male–male contests in the sexually dimorphic Wellington tree weta. *Animal Behaviour*, 72(3), 727–736.
<https://doi.org/10.1016/j.anbehav.2006.02.007>
- Kelly, C. D., & L’Heureux, V. (2021). Effect of diet and rearing density on contest outcome and settlement in a field cricket. *Behavioral Ecology and Sociobiology*, 75(3), 50.
<https://doi.org/10.1007/s00265-021-02990-w>
- Khazraïe, K., & Campan, M. (1999). The role of prior agonistic experience in dominance relationships in male crickets *Gryllus bimaculatus* (Orthoptera: Gryllidae). *Behavioural Processes*, 44(3), 341–348. [https://doi.org/10.1016/S0376-6357\(98\)00058-8](https://doi.org/10.1016/S0376-6357(98)00058-8)
- Kimber, B., & McDonald, G. (2015). Black Field Crickets *Teleogryllus commodus*. *Pest Notes Southern 1*: 1-5.
- Kodric-Brown, A., & Brown, J. H. (2015). Truth in Advertising: The Kinds of Traits Favored by Sexual Selection. *The American Naturalist*. <https://doi.org/10.1086/284275>
- Kodric-Brown, A., Sibly, R. M., & Brown, J. H. (2006). The allometry of ornaments and weapons. *Proceedings of the National Academy of Sciences*, 103(23), 8733–8738.
<https://doi.org/10.1073/pnas.0602994103>
- Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W., & Blokhuis, H. J. (1999). Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews*, 23(7), 925–935.
[https://doi.org/10.1016/S0149-7634\(99\)00026-3](https://doi.org/10.1016/S0149-7634(99)00026-3)
- Kortet, R., & Hedrick, A. (2007). A behavioural syndrome in the field cricket *Gryllus integer*: Intrasexual aggression is correlated with activity in a novel environment. *Biological Journal of the Linnean Society*, 91(3), 475–482. <https://doi.org/10.1111/j.1095-8312.2007.00812.x>

- Lihoreau, M., Brepson, L., & Rivault, C. (2009). The weight of the clan: Even in insects, social isolation can induce a behavioural syndrome. *Behavioural Processes*, 82(1), 81–84.
<https://doi.org/10.1016/j.beproc.2009.03.008>
- Linsdale, J., & Tomich, P. (1953). A Herd of Mule Deer, 511f. *Univ. of California Press, Berkeley and Los Angeles*.
- Lobregat, G., Kloss, T. G., Peixoto, P. E. C., & Sperber, C. F. (2019). Fighting in rounds: Males of a neotropical cricket switch assessment strategies during contests. *Behavioral Ecology*, 30(3), 688–696. <https://doi.org/10.1093/beheco/arz005>
- Ma, Libin, He, Zhuqing, & Zhang, Ya-Lin. (2015). Taxonomy of Chinese black field crickets *Teleogryllus Chopard* (Grylloidea, Gryllinae) with new distribution record of the exotic species *Teleogryllus commodus* (Walker). *Journal of Shaanxi Normal University (Natural Science Edition)*. 43. 10.15983/j.Cnki.Jsnu.2015.03.334.
- Magara, H. J. O., Niassy, S., Ayieko, M. A., Mukundamago, M., Egonyu, J. P., Tanga, C. M., Kimathi, E. K., Ongere, J. O., Fiaboe, K. K. M., Hugel, S., Orinda, M. A., Roos, N., & Ekesi, S. (2021). Edible Crickets (*Orthoptera*) Around the World: Distribution, Nutritional Value, and Other Benefits—A Review. *Frontiers in Nutrition*, 0. <https://doi.org/10.3389/fnut.2020.537915>
- Magurran, A. E. (1992). *Behaviour of Teleost Fishes*. Springer Science & Business Media.
- Martin, J. G. A., & Réale, D. (2008). Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Animal Behaviour*, 75(1), 309–318.
<https://doi.org/10.1016/j.anbehav.2007.05.026>
- Maynard Smith, J., & Parker, G. A. (1976). The logic of asymmetric contests. *Animal Behaviour*, 24(1), 159–175. [https://doi.org/10.1016/S0003-3472\(76\)80110-8](https://doi.org/10.1016/S0003-3472(76)80110-8)
- Maynard Smith, & Price, G. R. (1973). The logic of Animal Conflict. *Nature*, 246, pages15-18.
<https://doi.org/10.1038/246015a0>

- McCambridge, J. E., Painting, C. J., Walker, L. A., & Holwell, G. I. (2022). Contests between male New Zealand sheet-web spiders, *Cambridgea plagiata* (Araneae: Desidae). *New Zealand Journal of Zoology*, 49(1), 53–66. <https://doi.org/10.1080/03014223.2021.1909081>
- Mesterton-Gibbons, M., Marden, J. H., & Dugatkin, L. A. (1996). On Wars of Attrition Without Assessment. *Journal of Theoretical Biology*, 181(1), 65–83.
<https://doi.org/10.1006/jtbi.1996.0115>
- Michelangeli, M., Chapple, D. G., Goulet, C. T., Bertram, M. G., & Wong, B. B. M. (2019). Behavioral syndromes vary among geographically distinct populations in a reptile. *Behavioral Ecology*, 30(2), 393–401. <https://doi.org/10.1093/beheco/ary178>
- Montealegre-Z, F., Jonsson, T., & Robert, D. (2011). Sound radiation and wing mechanics in stridulating field crickets (Orthoptera: Gryllidae). *Journal of Experimental Biology*, 214(12), 2105–2117. <https://doi.org/10.1242/jeb.056283>
- Moore, J. C., Obbard, D. J., Reuter, C., West, S. A., & Cook, J. M. (2008). Fighting strategies in two species of fig wasp. *Animal Behaviour*, 76(2), 315–322.
<https://doi.org/10.1016/j.anbehav.2008.01.018>
- Morrell, L. J., Backwell, P. R. Y., & Metcalfe, N. B. (2005). Fighting in fiddler crabs *Uca mjoebergi*: What determines duration? *Animal Behaviour*, 70(3), 653–662.
<https://doi.org/10.1016/j.anbehav.2004.11.014>
- Mowles, S. L., Cotton, P. A., & Briffa, M. (2012). Consistent crustaceans: The identification of stable behavioural syndromes in hermit crabs. *Behavioral Ecology and Sociobiology*, 66(7), 1087–1094. <https://doi.org/10.1007/s00265-012-1359-7>
- Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, 85(4), 935–956. <https://doi.org/10.1111/j.1469-185X.2010.00141.x>

- Niemelä, P. T., DiRienzo, N., & Hedrick, A. V. (2012). Predator-induced changes in the boldness of naïve field crickets, *Gryllus integer*, depends on behavioural type. *Animal Behaviour*, 84(1), 129–135. <https://doi.org/10.1016/j.anbehav.2012.04.019>
- Niemelä, P. T., Lattenkamp, E. Z., & Dingemanse, N. J. (2015). Personality-related survival and sampling bias in wild cricket nymphs. *Behavioral Ecology*, 26(3), 936–946. <https://doi.org/10.1093/beheco/arv036>
- Olvido, A. E., & Wagner, W. E., Jr. (2004). Signal components, acoustic preference functions and sexual selection in a cricket. *Biological Journal of the Linnean Society*, 83(4), 461–472. <https://doi.org/10.1111/j.1095-8312.2004.00404.x>
- Painting, C. J., Buckley, T. R., & Holwell, G. I. (2014). Male-biased sexual size dimorphism and sex ratio in the New Zealand Giraffe Weevil, *Lasiorhynchus barbicornis* (Fabricius, 1775) (Coleoptera: Brentidae). *Austral Entomology*, 53(3), 317–327. <https://doi.org/10.1111/aen.12080>
- Painting, C. J., & Holwell, G. I. (2014). Exaggerated rostra as weapons and the competitive assessment strategy of male giraffe weevils. *Behavioral Ecology*, 25(5), 1223–1232. <https://doi.org/10.1093/beheco/aru119>
- Parker, G. A. (1974). Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology*, 47(1), 223–243. [https://doi.org/10.1016/0022-5193\(74\)90111-8](https://doi.org/10.1016/0022-5193(74)90111-8)
- Payne. (1998). Gradually escalating fights and displays: The cumulative assessment model. *Animal Behaviour*, 56(3), 651–662. <https://doi.org/10.1006/anbe.1998.0835>
- Payne, & Pagel. (1996). Escalation and Time Costs in Displays of Endurance. *Journal of Theoretical Biology*, 183(2), 185–193. <https://doi.org/10.1006/jtbi.1996.0212>

- Peixoto, P. E. C., & Benson, W. W. (2012a). Influence of previous residency and body mass in the territorial contests of the butterfly *Hermeuptychia fallax* (Lepidoptera: Satyrinae). *Journal of Ethology*, 30(1), 61–68. <https://doi.org/10.1007/s10164-011-0294-9>
- Peixoto, P. E. C., & Benson, W. W. (2012b). Influence of previous residency and body mass in the territorial contests of the butterfly *Hermeuptychia fallax* (Lepidoptera: Satyrinae). *Journal of Ethology*, 30(1), 61–68. <https://doi.org/10.1007/s10164-011-0294-9>
- Pinto, N. S., Palaoro, A. V., & Peixoto, P. E. C. (2019). All by myself? Meta-analysis of animal contests shows stronger support for self than for mutual assessment models. *Biological Reviews*, 94(4), 1430–1442. <https://doi.org/10.1111/brv.12509>
- Pinto, N. S., & Peixoto, P. E. C. (2019). What do we need to know to recognize a contest? *The Science of Nature*, 106(7), 32. <https://doi.org/10.1007/s00114-019-1632-y>
- Prenter, J., Elwood, R. W., & Taylor, P. W. (2006). Self-assessment by males during energetically costly contests over precopula females in amphipods. *Animal Behaviour*, 72(4), 861–868. <https://doi.org/10.1016/j.anbehav.2006.01.023>
- Prenter, J., Taylor, P. W., & Elwood, R. W. (2008). Large body size for winning and large swords for winning quickly in swordtail males, *Xiphophorus helleri*. *Animal Behaviour*, 75(6), 1981–1987. <https://doi.org/10.1016/j.anbehav.2007.12.008>
- Price, T., & Langen, T. (1992). Evolution of correlated characters. *Trends in Ecology & Evolution*, 7(9), 307–310. [https://doi.org/10.1016/0169-5347\(92\)90229-5](https://doi.org/10.1016/0169-5347(92)90229-5)
- R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. RStudio: Integrated Development for R. RStudio, R Foundation for Statistical Computing. <https://www.R-project.org/>
- Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population

level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4051–4063. <https://doi.org/10.1098/rstb.2010.0208>

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>

Reaney, L. T., Drayton, J. M., & Jennions, M. D. (2011). The role of body size and fighting experience in predicting contest behaviour in the black field cricket, *Teleogryllus commodus*. *Behavioral Ecology and Sociobiology*, 65(2), 217–225. <https://doi.org/10.1007/s00265-010-1030-0>

Ritz, M. S., & Köhler, G. (2010). Natural and sexual selection on male behaviour and morphology, and female choice in a wild field cricket population: Spatial, temporal and analytical components. *Evolutionary Ecology*, 24(5), 985–1001. <https://doi.org/10.1007/s10682-009-9328-y>

Roger, B. M. (1991). Game theory: Analysis of conflict. *The President and Fellows of Harvard College*.

Rose, J., Cullen, D. A., Simpson, S. J., & Stevenson, P. A. (2017). Born to win or bred to lose: Aggressive and submissive behavioural profiles in crickets. *Animal Behaviour*, 123, 441–450. <https://doi.org/10.1016/j.anbehav.2016.11.021>

Royauté, R., Garrison, C., Dalos, J., Berdal, M. A., & Dochtermann, N. A. (2019). Current energy state interacts with the developmental environment to influence behavioural plasticity. *Animal Behaviour*, 148, 39–51. <https://doi.org/10.1016/j.anbehav.2018.11.013>

Royauté, R., Greenlee, K., Baldwin, M., & Dochtermann, N. A. (2015). Behaviour, metabolism and size: Phenotypic modularity or integration in *Acheta domesticus*? *Animal Behaviour*, 110, 163–169. <https://doi.org/10.1016/j.anbehav.2015.09.027>

- Rudin, F. S., & Briffa, M. (2012). Is boldness a resource-holding potential trait? Fighting prowess and changes in startle response in the sea anemone, *Actinia equina*. *Proceedings of the Royal Society B: Biological Sciences*, 279(1735), 1904–1910.
<https://doi.org/10.1098/rspb.2011.2418>
- Rudin, F. S., Tomkins, J. L., & Simmons, L. W. (2017). Changes in dominance status erode personality and behavioral syndromes. *Behavioral Ecology*, 28(1), 270–279.
<https://doi.org/10.1093/beheco/arw151>
- Salazar, S. M., García, J. I. C., Kuspiel, M., Fokkema, R. W., Komdeur, J., & Korsten, P. (2021). Male aggressiveness and risk-taking during reproduction are repeatable but not correlated in a wild bird population. *Behavioral Ecology and Sociobiology*, 75(7), 108.
<https://doi.org/10.1007/s00265-021-03044-x>
- Santostefano, F., Wilson, A. J., Araya-Ajoy, Y. G., & Dingemanse, N. J. (2016). Interacting with the enemy: Indirect effects of personality on conspecific aggression in crickets. *Behavioral Ecology*, 27(4), 1235–1246. <https://doi.org/10.1093/beheco/arw037>
- Scharf, I., Stoldt, M., Libbrecht, R., Höpfner, A. L., Jongepier, E., Kever, M., & Foitzik, S. (2021). Social isolation causes downregulation of immune and stress response genes and behavioural changes in a social insect. *Molecular Ecology*, 30(10), 2378–2389.
<https://doi.org/10.1111/mec.15902>
- Schnell, A. K., Smith, C. L., Hanlon, R. T., & Harcourt, R. (2015). Giant Australian cuttlefish use mutual assessment to resolve male-male contests. *Animal Behaviour*, 107, 31–40.
<https://doi.org/10.1016/j.anbehav.2015.05.026>
- Shackleton, M. A., Jennions, M. D., & Hunt, J. (2005). Fighting success and attractiveness as predictors of male mating success in the black field cricket, *Teleogryllus commodus*: The

effectiveness of no-choice tests. *Behavioral Ecology and Sociobiology*, 58(1), 1–8.

<https://doi.org/10.1007/s00265-004-0907-1>

Shaw, C. E. (1948). The Male Combat “Dance” of Some Crotalid Snakes. *Herpetologica*, 4(4), 137–145.

Shaw, C. E. (1951). Male Combat in American Colubrid Snakes with Remarks on Combat in Other Colubrid and Elapid Snakes. *Herpetologica*, 7(4), 149–168.

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372–378.

<https://doi.org/10.1016/j.tree.2004.04.009>

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral Syndromes: An Integrative Overview. *The Quarterly Review of Biology*, 79(3), 241–277. <https://doi.org/10.1086/422893>

Sih, A., Mathot, K. J., Moirón, M., Montiglio, P.-O., Wolf, M., & Dingemanse, N. J. (2015). Animal personality and state–behaviour feedbacks: A review and guide for empiricists. *Trends in Ecology & Evolution*, 30(1), 50–60. <https://doi.org/10.1016/j.tree.2014.11.004>

Simmons, L. W. (1986). Female choice in the field cricket *Gryllus bimaculatus* (De Geer). *Animal Behaviour*, 34(5), 1463–1470. [https://doi.org/10.1016/S0003-3472\(86\)80217-2](https://doi.org/10.1016/S0003-3472(86)80217-2)

Sneddon, L. U. (2003). The bold and the shy: Individual differences in rainbow trout. *Journal of Fish Biology*, 62(4), 971–975. <https://doi.org/10.1046/j.1095-8649.2003.00084.x>

Stahlschmidt, Z., O’Leary, M. E., & Adamo, S. (2014). Food limitation leads to risky decision making and to tradeoffs with oviposition. *Behavioral Ecology*, 25(1), 223–227.

<https://doi.org/10.1093/beheco/art110>

Stapley, J., & Keogh, J. S. (2005). Behavioral syndromes influence mating systems: Floater pairs of a lizard have heavier offspring. *Behavioral Ecology*, 16(3), 514–520.

<https://doi.org/10.1093/beheco/ari019>

- Stuart-Fox, D. (2006). Testing game theory models: Fighting ability and decision rules in chameleon contests. *Proceedings of the Royal Society B: Biological Sciences*, 273(1593), 1555–1561.
<https://doi.org/10.1098/rspb.2006.3468>
- Stuart-Fox, D. M., & Johnston, G. R. (2005). Experience overrides colour in lizard contests. *Behaviour*, 142(3), 329–350. <https://doi.org/10.1163/1568539053778265>
- Sun, C., Zhang, C., Gu, H., Jiang, T., & Feng, J. (2019). Self-assessment strategy during contest decisions between male Great Himalayan leaf-nosed bats. *Behavioral Ecology and Sociobiology*, 73(4), 45. <https://doi.org/10.1007/s00265-019-2657-0>
- Tan, M. K., Chang, C., & Tan, H. T. W. (2018). Shy herbivores forage more efficiently than bold ones regardless of information-processing overload. *Behavioural Processes*, 149, 52–58.
<https://doi.org/10.1016/j.beproc.2018.02.003>
- Taylor, P. W., & Elwood, R. W. (2003). The mismeasure of animal contests. *Animal Behaviour*, 65(6), 1195–1202. <https://doi.org/10.1006/anbe.2003.2169>
- Taylor, P. W., Hasson, O., & Clark, D. L. (2001). Initiation and resolution of jumping spider contests: Roles for size, proximity, and early detection of rivals. *Behavioral Ecology and Sociobiology*, 50(5), 403–413. <https://doi.org/10.1007/s002650100390>
- Tedore, C., & Johnsen, S. (2015). Visual mutual assessment of size in male *Lyssomanes viridis* jumping spider contests. *Behavioral Ecology*, 26(2), 510–518.
<https://doi.org/10.1093/beheco/aru222>
- Thomas, J. M. C. (2003). “Insects” in oral literature and traditions. *Peeters Publishers*.
- Thomas, M. L., & Simmons, L. W. (2010). Cuticular hydrocarbons influence female attractiveness to males in the Australian field cricket, *Teleogryllus oceanicus*. *Journal of Evolutionary Biology*, 23(4), 707–714. <https://doi.org/10.1111/j.1420-9101.2010.01943.x>

- Thurmond, J. B. (1975). Technique for producing and measuring territorial aggression using laboratory mice. *Physiology & Behavior*, 14(6), 879–881. [https://doi.org/10.1016/0031-9384\(75\)90086-4](https://doi.org/10.1016/0031-9384(75)90086-4)
- Toms, C. N., Echevarria, D. J., & Jouandot, D. J. (2010). A Methodological Review of Personality-Related Studies in Fish: Focus on the Shy-Bold Axis of Behavior. *International Journal of Comparative Psychology*, 23(1). <https://escholarship.org/uc/item/949413qt>
- Traisnel, G., & Pichegru, L. (2019). Boldness at the nest predicts foraging and diving behaviour of female but not male African penguins. *Animal Behaviour*, 150, 113–125. <https://doi.org/10.1016/j.anbehav.2019.02.003>
- Veneables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S* (4th ed.). Springer. <https://www.stats.ox.ac.uk/pub/MASS4/>
- Weissman, D. B., Gray, D. A., Pham, H. T., & Tijssen, P. (n.d.). Billions and billions sold: Pet-feeder crickets (*Orthoptera: Gryllidae*), commercial cricket farms, an epizootic densovirus, and government regulations make for a potential disaster. *TERMS OF USE*, 22.
- Westneat, D. F., Schofield, M., & Wright, J. (2013). Parental behavior exhibits among-individual variance, plasticity, and heterogeneous residual variance. *Behavioral Ecology*, 24(3), 598–604. <https://doi.org/10.1093/beheco/ars207>
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, Golemund, Hayes, Hester, Kuhn, Pedersen, Miller, Bach, Muller, Ooms, Robinson, Seidel, Spinu, Takahashi, ... Yutani. (2019). Welcome to {tidyverse}. *Journal of Open Source Software*, 4(43), 1686. <https://doi.org/10.21105/joss.01686>
- Wilson, A. D. M., Whattam, E. M., Bennett, R., Visanuvimol, L., Lauzon, C., & Bertram, S. M. (2010). Behavioral correlations across activity, mating, exploration, aggression, and antipredator

contexts in the European house cricket, *Acheta domesticus*. *Behavioral Ecology and Sociobiology*, 64(5), 703–715. <https://doi.org/10.1007/s00265-009-0888-1>

Wilson, D. S. (1998). Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 353(1366), 199–205. <https://doi.org/10.1098/rstb.1998.0202>

Wong, K., Elegante, M., Bartels, B., Elkhayat, S., Tien, D., Roy, S., Goodspeed, J., Suciu, C., Tan, J., Grimes, C., Chung, A., Rosenberg, M., Gaikwad, S., Denmark, A., Jackson, A., Kadri, F., Chung, K. M., Stewart, A., Gilder, T., ... Kalueff, A. V. (2010). Analyzing habituation responses to novelty in zebrafish (*Danio rerio*). *Behavioural Brain Research*, 208(2), 450–457. <https://doi.org/10.1016/j.bbr.2009.12.023>

Zeileis, A., & Hothorn, T. (2002). Diagnostic Checking in Regression Relationships. *R News*, 2(3), 7–10.

Zucker, N., & Murray, L. (1996). Determinants of Dominance in the Tree Lizard *Urosaurus ornatus*: The Relative Importance of Mass, Previous Experience and Coloration. *Ethology*, 102(6), 812–825. <https://doi.org/10.1111/j.1439-0310.1996.tb01203.x>