The impact of intraspecific predation on individual fitness and population viability

CONTENTS

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‡ Deceased

Ψ Escaped

The original idea for this thesis was conceived whilst I was working (voluntarily) in the behavioural ecology lab at Macquarie University, Sydney. My initial thoughts for the project centred around investigating the ways in which the environment might change such that sexual cannibalism increased population extinction risk. Whilst this is the running theme throughout the work presented here, I also, in various places, allude to the notion that there may be many reproductive behaviours that could very quickly become maladaptive in response to rapid environmental change*. As I am keen to publish most, if not all of the data chapters in this thesis, each chapter is written independently of the others and structured in the style of a paper.

The introduction gives an overview of the main taxonomic groups known to display cannibalism and the types of cannibalism formally reported in the literature. It is structured so that each section describes a particular scenario that is likely to provide cues that affect cannibalism rates in some species. For example, the effect of low nutrient availability on the frequency of cannibalism. In each section I then go on to talk about how, if cannibalism rates do change in response to this cue, the environment might dictate the population level effects of cannibalism. In particular, I predict what the effects of rapid reductions in population size and density may have on the population-level impacts of cannibalism.

Chapter 1 lays some theoretical groundwork regarding the impact of sexual cannibalism on population extinction risk and per capita growth rate. Here I consider how the population-level effects of cannibalism are affected by: 1) cannibalism rate, 2) cannibalism type, and 3) the amount of fecundity benefits a female can gain from cannibalising a male. In 2018 the paper was published in Ecology and Evolution.

Chapter 2 is another theoretical study that investigates whether Allee effects can occur as a result of sexual cannibalism. I independently test for the effects of population size and density on extinction risk. Once again, I compare differences between cannibalism type and the amount of fecundity benefits a female can gain from devouring a male. At the time of writing this manuscript is under review at the Journal of Animal Ecology.

Chapter 3 is composed of findings from the first bit of lab work I did during the PhD which attempted to explore the link between perceived mate density and aggression in female fen raft spiders (*Dolomedes fimbriatus*). It is probably the worst of all of my data chapters. This is partly because the sample size is pretty low due to difficulties getting permission from Natural England to collect enough spiders. Also, females were not very aggressive, so the main finding is non-significant. However, I did find two surprising outcomes that I think are fairly interesting. At the time of writing the paper is under review in Arachnology.

Chapter 4 investigated the link between sexual cannibalism and behavioural syndromes in two species of praying mantis. To do this, I measured whether aggression was repeatable within individuals, across lifestages and across contexts. The work was carried out over two field seasons at the University of Auckland, NZ with my co-supervisor Greg Holwell. The manuscript has recently been submitted to Behavioural Ecology and Sociobiology.

Chapter 5 looks at cannibalism rates in larval *Drosophila*. Specifically, we looked at how cannibalism rates are affected by starvation, genetic relatedness and conspecific density. The results of this project are extremely strange in that they actually turned out how I expected them to, something I didn't think could happen in scientific studies.

*I don't claim that this theory is my own. However, there is surprisingly little work on this. Two resources that I have found particularly useful are the paper "Evolution and behavioural responses to human-induced rapid environmental change" by Sih and others (2011), and the book "Conservation behaviour" by Berger-Tal & Saltz.

INTRODUCTION: Predatory cannibalism and its effect on small or sparse populations

Predatory cannibalism, the devouring of living conspecifics, is a significant source of mortality for populations across a range of taxonomic groups. Among the most frequently studied cannibalistic groups are spiders (Elgar, 1991; Arnqvist, 1992; Andrade, 1996; Hernández et al., 2018), insects (Via, 1999; Vijendravarma at al., 2013; Walker & Holwell, 2015), fish (Pereira, 2017; Dassow et al., 2018; Colchen et al., 2019) and amphibians (Pfennig, 1999; Markman et al., 2009). In the past, cannibalism was often regarded as an artefact of laboratory conditions. While certain lab conditions, such as overcrowding, undoubtedly encourage cannibalism (Sogard & Olla, 1994), there is now a wealth of field-based evidence supporting the idea that cannibalism is natural (Fox, 1975; Lawrence, 1992; Rabaneda-Bueno et al., 2008; Dassow et al., 2018; Bose et al., 2019). Cannibalism has been fairly well-studied in terms of its effect on individual fitness (Via, 1999; Schwartz et al., 2016); in addition, there are numerous studies that investigate the population-level effects of cannibalism when populations are large and dense (Ricker, 1954; Claessen et al., 2004). However, very little is known about the population-level effects of cannibalism when it occurs in damaged and impoverished habitats, where populations are likely to be small and sparse. This thesis mainly focuses on the potential impact of cannibalism at the population level. Here, I will provide an overview of the hypotheses for why cannibalism occurs in nature, highlight gaps in the current knowledge and provide insights into the impact of cannibalism on small or sparse populations.

Cannibalism can take several forms, and examples used in this review fall into three main categories: 1) inter-cohort cannibalism, 2) intra-cohort cannibalism, and 3) sexual cannibalism. Most examples of inter-cohort cannibalism come from work on teleost fish, where filial cannibalism is common (Vallon et al., 2016; Pereira et al., 2017). But there are also examples of inter-cohort cannibalism in fruit flies, where larvae eat eggs (Narasimha et

al., 2019) and spiders, where adults eat juveniles (de Carvalho Guimarães et al., 2016).

There is less evidence for intra-cohort cannibalism in fish, perhaps because there is a higher

risk of victim-inflicted injury or a greater chance of victim escaping if they are of a similar

size and age (Polis, 1981; Petranka & Thomas, 1995). Nevertheless, intra-cohort

cannibalism is common in some species of carnivorous fish (Baras et al., 2000; Colchen et

al., 2019), amphibians (Pfennig et al., 1993; Hoffman & Pfennig, 1999) and invertebrates

(Bilde & Lubin, 2001; Dobler & Kölliker, 2009; Fea et al., 2014). Sexual cannibalism typically

involves a female cannibalising a male, immediately before, during or after copulation, and

has mainly been observed in praying mantids and spiders (Elgar, 1992). Although sexual

cannibalism is a type of intra-cohort cannibalism, we define it separately due to the more

direct impact it can have on reproductive success (Barry et al., 2008; Schwartz et al., 2016).

Cannibalism is often regarded as an extreme behaviour owing to the potential fitness costs

it can incur on victims and the effects it can have at the population-level. Different types of

cannibalism will undoubtedly vary in-terms of how they affect individual fitness and

population ecology, and these effects may be dependent on the environment. For example,

filial cannibalism has been shown to have a stabilising effect on population dynamics at

high densities by limiting fluctuations in intraspecific competition (Rich, 1956; Kolmeier &

Ebenhöh, 1995). Conversely, high cannibalism rates among adults may lead to the death of

potential reproductive partners and an increase in virgin death rates, particularly at low

population densities (Fisher et al., 2018; Fisher et al., unpublished data). Understanding

how the impact of cannibalism at the population-level changes in response to the

environment will be important for predicting how habitat change will affect the viability of

cannibalistic populations. Moreover, understanding the environmental cues that trigger

cannibalistic behaviour, will help predict if and how cannibalism rates will change in

response to the environment.

Identifying the selective pressures that have caused cannibalism to evolve is vital for predicting how the frequency of cannibalism will change with environmental changes (Wilder et al., 2009). If cannibalism evolved as a mechanism to gain nutrients when alternative food sources are scarce, then we might expect a higher frequency of cannibalism in populations where high levels of competition leads to low prey availability. Similarly, in the case of pre-copulatory cannibalism, individuals may be selected to be less cannibalistic when mate availability is low to reduce their risk of dying without mating. There is evidence from spiders that females are less likely to attack potential mates when males are perceived to be rare (Johnson, 2004; Wilder et al., 2009). However, an overlooked issue is that some environmental variables that cause cannibalism to be beneficial may be correlated with other environmental variables that cause cannibalism to be maladaptive (Fisher et al., 2018), potentially creating an evolutionary trap (Schlaepfer et al., 2002). For example, if both nutrient availability and mate availability are reduced, then individuals who increase their cannibalism rates in response to nutrients may run the risk of dying a virgin and further reduce the number of reproductive individuals in the population (Box 1). This could be a realistic scenario given that females of some cannibalistic species are known to attract fewer males when partially starved (Barry, 2010; Barry, 2013; Johnson et al., 2011), meaning cannibalism rates may increase in response to starvation despite decreasing male availability. Problems like this could become more common if habitat quality is rapidly reduced through large disturbances such as those commonly caused by humans. Therefore, understanding the environmental triggers of cannibalism may become increasingly important for species conservation.

This review is structured such that each section focusses on a specific environmental challenge that cannibalism may have evolved to overcome. In each section, we outline some of the evidence that supports the hypothesis that cannibalism evolved in response to the environmental challenge in question. Often, this evidence takes the form of cannibalism rates varying in response to specific environmental cues. We then suggest the implications that cannibalism may have for population viability in poor or damaged habitats if cannibalism rates continue to be strictly determined by those environmental cues. In

some cases, this exposes gaps in the current literature, thus we provide some advice on potential directions for future work.

Nutrient availability

In any instance of cannibalism, the individual cannibalising is likely to receive some degree of nutritional benefit. Evidence suggesting this has come from studies that have observed decreased developmental time (Michaud, 2003), longer survival times (Yahsuda & Ohnuma, 1999; Michaud, 2003) and increased fecundity in cannibalistic individuals (Barry et al., 2008; Schwartz et al., 2016). In addition, cannibalism rates are often negatively associated with the supply of alternative food sources, implying that cannibalism can be used as a mechanism for gaining nutrition when nutrients are rare (Folkvord, 1991; Barry et al., 2008; Vijendravarma et al., 2013). For example, in spotted seatrout (*Cynoscion nebulosus*) larvae, starved individuals were significantly more likely to attack conspecifics (Manley et al., 2015). Increased rates of cannibalism in response to starvation has also been shown in larvae of the fruit fly *Drosophila melanogaster* (Vijendravarma et al., 2013) and adults of the praying mantis *Pseudomantis albofimbriata* (Barry et al., 2008). Cannibalism may also facilitate increased activity levels as is seen in the common goby (*Pomatoschistus microps*) (Vallon, 2016).

The degree to which cannibalism is nutritionally beneficial is likely to be species–specific. Thus, the nutrition a single victim can provide and the frequency of cannibalism will be fundamental for determining nutritional benefit. For inter-cohort cannibalism, it may be that cannibals must eat many individuals in order to receive a substantial benefit (Rich, 1956; Pereira et al., 2017). For example, in the South African anchovy, cannibalism is responsible for ≈70% of egg mortality (Valdés, 1987). In sexually cannibalistic species, females can benefit from increased fecundity by devouring a single male, for example female dark fishing spiders (*Dolomedes tenobrosus*) produce almost twice as many offspring when they devour a male post-copulation (Scwartz et al., 2016). But even in intra-

cohort cannibalism, the nutritional benefit of eating conspecifics can be small due to large sexual dimorphism. For example, female orb-weaving spiders of the genus *Nephila* regularly cannibalise males that attempt to copulate, but the body mass of males is only ≈ 10% of the female's, making their nutrient value almost negligible (Schneider & Elgar, 2001; Schneider & Elgar, 2002). In cases where devouring males provides no detectable fitness benefits for females it is sometimes thought that cannibalism may be initiated by males to maximise their paternity. Male redback spiders (*Latrodectus hasselti*) sacrifice themselves after copulation to delay the female remating (Andrade, 1996; Andrade, 2003).

Cannibalism is known to provide a significant nutritional benefit for certain species, which may increase survival rates when alternative food sources are scarce. Food availability is subject to spatial variation, so cannibalism may have evolved to provide individuals with an opportunity to expand their range into nutrient poor environments (Via, 1999). In addition, historic temporal fluctuations in nutrient availability may also select for cannibalism. Fluctuations in food availability can be caused by several ecological scenarios. One of the most studied causes of food limitation is high levels of intra-specific competition. Such scenarios are common in laboratory or aquaculture settings where there are many individuals in confined spaces (Van Buskirk, 1989; Hopper et al., 1996); but high densities may also occur in the wild and lead to increased cannibalism rates (Guttal et al., 2012).

Food limitation can also occur as a consequence of habitat degradation (Watson, 2011). As discussed earlier, habitat degradation could create environmental scenarios such as low mate availability which occur in concert with low nutrient availability and cause cannibalism to become maladaptive (see Box 1; Fisher et al., 2019). To determine whether or not this could be a problem for cannibalistic populations, it is important to know whether cannibalistic individuals can assess multiple environmental cues and alter their rate of cannibalism to maximise fecundity in specific environments. Individuals will be more

likely to be able to respond to environmental cues associated with disturbance if they have encountered heavy disturbance in their recent evolutionary history (Sih et al., 2011). Further experimental work assessing how cannibalistic individuals prioritise certain environmental cues would be valuable for helping to predict cannibalism rates in changing environments.

Mate quality

Cannibalism, specifically sexual cannibalism, can be used as a mechanism for selecting mates (Prenter et al., 2006). There is evidence from several groups of spiders that the probability of females cannibalising males prior to copulation is related to male condition. Male brush-legged wolf spiders (*Schizocosa ocreata*) perform courtship displays which consist of the rhythmic tapping of their bristle-covered forelegs (Stratton & Uetz, 1983). The size of the tufts on the male's forelegs are an indicator of overall body condition and are thought to have evolved as a secondary sexual characteristic to signal quality (Uetz et al., 2002). As such, males with larger tufts are less likely to be cannibalised by females (Persons & Uetz, 2005). The relationship between sexually selected male traits and cannibalism implies that mate choice in *S. ocreata* is likely to be direct – i.e. females actively avoid attacking males that appear to be of better quality. However, apparent mate choice in other species may simply be a product of certain males being better able to escape female predation. Females of certain species of fishing spider (family: Pisauridae) attempt to attack all of the males they encounter, but larger males are more likely to escape (Arnqvist, 1992; Johnson, 2001) and gain more copulations (Arnqvist, 1992). As females attack nearly all males that attempt to copulate, it seems unlikely that females are assessing male quality before attacking.

Regardless of whether females choose males based on sexual cues, or if larger males are simply better at evading cannibalism, males in poor condition are less likely to mate. This creates the possibility of decreased mating rates in degraded habitats, where males are

smaller due to lower feeding rates (Uetz et al., 2002). This could lead to increased female virgin death rates and an increased probability of population extinction (Fisher et al., 2018; Fisher et al., 2019). Obviously, food availability fluctuates year-on-year and does not necessarily cause population crashes in cannibalistic species, implying that a minimum number of individuals still mate successfully even in 'bad' years. However, if rapid human-induced habitat change causes the environment to shift outside of the 'normal' limits experienced in an organism's recent evolutionary history, then some species may not be equipped to modify their behaviour in a way that minimises loss of fitness and extinction risk (Sih et al., 2011). As of yet, there has been no formal investigation into how the quality of males a female has previously encountered affects her tendency to cannibalise. However, this information would be valuable in predicting the behaviour of females in a population where male quality is abnormally low.

One way in which species using cannibalism for mate choice may be more robust to habitat change is if cannibalism rates are plastic with regards to average male quality. For example, if females choose males based on their size relative to other males instead of absolute size, males could remain attractive even under nutritional stress. As mentioned earlier, females in some species can alter their rates of cannibalism in response to perceived mate availability; but, plasticity in response to average male quality has not yet been demonstrated. It could be that it is impossible for females to gather information on the average size of males in the population due to male-female encounters being sequential (Barry & Kokko, 2010). Because both male and female size are likely to be affected by feeding rates, cannibalism rate may be unaffected by poor habitat quality if cannibalism is determined by male size relative to the female as oppose to absolute male size. Absolute male size and male size relative to females are likely to be correlated, making it difficult to tease apart which is more important for determining cannibalism. However, there is some

evidence to say that males which are relatively larger will be less likely to be cannibalised (Persons & Uetz, 2005; Prenter et al., 2006).

Size asymmetry

In the majority of species that are known to exhibit cannibalism, cannibals are larger than their victims (Polis, 1981; Pereira, 2017), although there are some exceptions (Baras et al., 2000; Fea et al., 2014; Yang et al., 2015). This trend is likely to largely be due to a higher capture success rate and a lower risk of injury associated with attacking smaller prey. The most common mechanism by which large size variation occurs is via overlapping generations in a population. Hence the most frequently observed type of cannibalism is that between cohorts (Persson et al., 2000). However, due to staggered emergence times and spatial variation in resource availability, there is often enough size variation within cohorts to facilitate cannibalism (Byström, 2012). In some species, sexual dimorphism is responsible for the size difference between cannibals in their victims; this is particularly true in species that exhibit sexual cannibalism, where it is typically the larger female that devours the male (Wilder & Rypstra, 2008). The trend is perhaps most apparent in orb-weaving spiders (Elgar, 1991), where an adult male can be 10% the mass of an adult female (Schneider & Elgar, 2001; Schneider & Elgar, 2002). The large size dimorphism observed in many spiders is often hypothesised to have evolved to facilitate sexual cannibalism by reducing the risk of injury to females (Wilder & Rypstra, 2008). However, there are numerous examples that do not fit this hypothesis, such as species where males and females are of a similar size but cannibalism still takes place (Lelito & Brown, 2008). Also, some species within clades where cannibalism is common display high levels of sexual dimorphism but sexual cannibalism is absent (Elgar et al., 1990). Nevertheless, the prevalence of sexual cannibalism in sexually dimorphic spiders strongly indicates that size asymmetry can help facilitate cannibalism (Wilder & Rypstra, 2008).

Another way in which size asymmetry can be achieved is through polyphenisms (i.e.

alternative phenotypes that can be achieved through a single genotype in response to

environmental cues (West-Eberhard, 1989)). The presence of cannibalistic and non-

cannibalistic phenotypes has been observed in the larvae of several species of amphibian,

and is thought to have evolved in response to the limited availability of alternative food

sources (Crump, 1992). There is evidence for several environmental cues that promote the

production of cannibalistic morphs in a population. In tiger salamander larvae (*Ambystoma*

tigrinum), over-crowding with conspecific and congeneric larvae is linked to an increase in

cannibalistic morphs. In nature, more crowded conditions may signal higher levels of

competition and thus lower food availability. Equally, cannibalistic morphs may simply be

triggered because high numbers of conspecifics signal a greater number of opportunities to

cannibalise. In spadefoot toad tadpoles, the frequency of cannibalistic morphs is directly

linked to the availability of fairy shrimp, the primary food source of the larvae (Pfennig,

1990). If the frequency of cannibalistic morphs is a direct result of a lack of food, then

cannibalism-induced mortality rates may increase in response to lower food availability not

only due to increased competition, but also due to lower habitat quality. As discussed in

other sections of this review, increased cannibalism in impoverished habitats may lead to

increased extinction risk (Fisher et al., 2018; Fisher et al., 2019). This is particularly true if,

like in the tiger salamander, the production of cannibalistic morphs is not frequency-

dependent (Hoffman & Pfennig, 1999). This could potentially lead to higher cannibalism

rates and accelerated mortality.

Relatedness

How an organism behaves towards related individuals can have large implications for the

inclusive fitness of the organism (Hamilton, 1964). As such, many species have evolved

mechanisms to allow them to detect relatives and behave towards them in a way that

optimises inclusive fitness. Mechanisms for assessing relatedness can be direct and involve

individuals detecting phenotypic traits that are linked to specific genes or genotypes (Lihoreau et al., 2007; Gardner, 2019). Alternatively, relatedness can be assessed indirectly through familiarity; for example, regarding individuals that you encounter early in life as kin (Ward & Hart, 2003; Hollis et al., 2015). Cannibals run the risk of killing a relative if they cannot discriminate between individuals based on relatedness. Thus we may expect strong selection for mechanisms that allow cannibals to recognise related individuals, particularly in species where the chance of encountering a relative is high.

Invertebrate larvae often emerge *en masse* with others from the same brood and can be carnivorous, creating a potential for siblicide. As such, evidence of kin recognition is seen in several invertebrate species (Nummelin, 1989, Fisher et al., 2019 unpublished data). European earwig larvae cannibalise non-kin more frequently than kin (Dobler & Kölliker, 2009); similarly, desert spiders preferentially cannibalise non-kin over kin when alternative food sources are scarce (Bilde & Lubin, 2001). There is also evidence from amphibians showing an effect of relatedness on cannibalism rates (Walls & Roudebush, 1991; Pfennig et al., 1994). Spadefoot toad larvae preferentially cannibalise non-kin over kin (Pfennig et al., 1993), and this preference becomes stronger if larvae develop into the larger cannibalistic morphs and become more dangerous for siblings (Pfennig, 1999). However, despite high cannibalism rates and a high probability of encountering relatives, there are several examples of cannibalistic species with no apparent kin recognition (Agarwala & Dixon, 1993). For example, nymphs of the highly cannibalistic springbok mantis (*Miomantis caffra*) demonstrate no preference between cannibalising kin and non-kin (Fea et al., 2014). A lack of selection for kin recognition in cannibalistic species could be due to high rates of female polyandry, reducing intra-brood relatedness. Also, it may be that in the wild, juveniles rapidly disperse after emergence making it unlikely that they will re-encounter kin.

Species where adults cannibalise eggs or juveniles run the risk of cannibalising their own offspring. Egg cannibalism is particularly common in fish, where males often provide parental care (Blumer, 1979). Thus males of many species have evolved to be able to assess their relatedness to egg clutches and reduce cannibalism of related offspring. Male three-spined sticklebacks (*Gasterosteus aculeatus*) can use egg cues to detect relatedness to a particular clutch and reduce cannibalism in response to increased relatedness to the brood (Mehlis et al., 2010). In species where male relatedness to a brood is uncertain, cannibalism may provide a way of removing offspring that have been sired by other males such that only related offspring receive parental investment. For example, male *Telmatherina sarasinorum* (a small fish endemic to Indonesia) increase the number of eggs they cannibalise as the number of competing males at spawning events increases (Gray et al., 2006). Even in species where males are not the primary care-givers, egg or juvenile cannibalism can still occur to ensure that female care is allocated only to related offspring. Famously, male lions will often kill the offspring of their new female partners (Packer, 2000) and similar behaviour is seen in some birds (Crook & Shields, 1985; Rohwear, 1986). Surprisingly, evidence of males killing the unrelated offspring of their female partners is rare, even in groups where parental care can be extremely costly; this is possibly due to successful female counter strategies (Packer & Pusey, 1983).

It is well documented that the genetic similarity between individuals can be associated with population size (Frankham, 1995). Therefore, in species where relatedness determines cannibalism rate, cannibalism may be influenced by population-level changes. In species such as the fire salamander (*Salamandra infraimmaculata*)**,** where cannibalism rate is negatively associated with genetic relatedness (Markman et al., 2009), individuals in smaller populations may cannibalise less. In species where brood relatedness is typically low due to high polyandry, a reduction in density may reduce mate encounter rate resulting in more closely related broods. Hence population density may also co-vary with

larval cannibalism rate if density is linked to mate availability. Reductions in population size and density caused by habitat disturbances such as fragmentation are of growing conservation concern. One could speculate that a decrease in mortality owing to lower cannibalism rates may partially offset the reduction in population viability that cannibalism could cause in small or sparse populations (Fisher et al., unpublished data).

Aggressive spillover

The aggressive spillover hypothesis states that cannibalism can be a by-product of selection for high aggression in other contexts, such as voracity towards non-conspecific prey (Arnqvist & Henriksson, 1997). This means that cannibalism may still evolve even if it is costly for the individual, provided that the benefits of being aggressive in other contexts outweigh the costs of cannibalism. As such, aggressive spillover has been used to explain examples of cannibalism that are apparently maladaptive. The majority of work advocating aggressive spillover has been carried out on fishing spiders (family: Pisauridae), where the female regularly attacks and kills the male prior to copulation, increasing her risk of dying a virgin. Johnson and Sih (2005) looked for evidence of aggressive spillover in the six-spotted fishing spider (*Dolomedes triton*) and found that voracity towards prey was indeed correlated with a propensity for pre-copulatory cannibalism. Other apparently maladaptive forms of cannibalism, such as the killing of one's own kin, may also be explained by aggressive spillover (Fea et al., 2014).

Where cannibalism is a by-product of selection for other behaviours, the environment is unlikely to directly influence frequency of cannibalism. If cannibalism rates cannot vary in response to environmental cues, then the behaviour may become extremely maladaptive under certain scenarios (Fisher et al., 2018; Fisher et al., 2019). For example, if females cannot lower cannibalism rates in response to low mate availability, the proportion of females that die as virgins may increase greatly in impoverished habitats. Moreover, if cannibalism is coupled with other behaviours, such as voracity towards prey, then certain

environments may inflict opposing selective pressures on individuals (Box 1). For example, individuals in impoverished habitats may be required to consume a wider variety of prey items, thus selecting for highly aggressive individuals. However, if there are fewer males due to a lack of resources, females should reduce their pre-copulatory cannibalism rate to accommodate for fewer mate encounters. Achieving viable levels for both behaviours in a declining habitat becomes more difficult if cannibalism and aggression towards prey are coupled in a way that prevents selection from acting upon the behaviours independently. Although there is behavioural evidence supporting the aggressive spillover hypothesis, there have been no formal investigations into the genetic basis for the coupling of aggression towards prey and potential mates. However, understanding whether the same genes cause both aggression towards prey and aggression towards potential mates would be valuable for predicting the evolution and persistence of each trait.

Conclusions

Cannibalism is a common natural phenomenon occurring in many taxonomic groups and can take several forms, ranging from the devouring of eggs to the killing of a potential reproductive partner. Across species, cannibalism is likely to have evolved in response to different environmental challenges, such as preventing starvation or choosing a suitable mate. As such, the environmental cues that influence cannibalism rate are likely to vary across species. In this review we have discussed some of the different environmental cues that trigger cannibalistic behaviour and have suggested how the magnitude of these cues may change in response to habitat change. In several examples we have highlighted how cannibalism rate may increase in response to reduced habitat quality and how this may exacerbate population decline. Specifically, opposing selective forces in poor quality habitats may create evolutionary traps in which individuals can no longer use cannibalism in a way that increases fitness. In doing this we draw attention to the potential relevance of cannibalism for conservation biology. We recommend that future work focuses on

exploring the plastic potential of cannibalism rates under certain perceived ecological

scenarios, these findings may then be used to inform population models predicting

population viability.

CHAPTER 1: Sexual cannibalism and population viability

Abstract

Some behaviours that typically increase fitness at the individual level may reduce population persistence, particularly in the face of environmental changes. Sexual cannibalism is an extreme mating behaviour which typically involves a male being devoured by the female immediately before, during or after copulation, and is widespread amongst predatory invertebrates. Although the individual-level effects of sexual cannibalism are reasonably well understood, very little is known about the population-level effects. We constructed both a mathematical model and an individual-based model to predict how sexual cannibalism might affect population growth rate and extinction risk. We found that in the absence of any cannibalism-derived fecundity benefit, sexual cannibalism is always detrimental to population growth rate and leads to a higher population extinction risk. Increasing the fecundity benefits of sexual cannibalism leads to a consistently higher population growth rate and likely a lower extinction risk. However, even if cannibalism-derived fecundity benefits are large, very high rates of sexual cannibalism (>70%) can still drive the population to negative growth and potential extinction. Pre-copulatory cannibalism was particularly damaging for population growth rates and was the main predictor of growth declining below the replacement rate. Surprisingly, post-copulatory cannibalism had a largely positive effect on population growth rate when fecundity benefits were present. This study is the first to formally estimate the population-level effects of sexual cannibalism. We highlight the detrimental effect sexual cannibalism may have on population viability if (1) cannibalism rates become high, and/or (2) cannibalism-derived fecundity benefits become low. Decreased food availability could plausibly both increase the frequency of cannibalism, and reduce the fecundity benefit of cannibalism, suggesting that sexual cannibalism may increase the risk of population collapse in the face of environmental change.

Introduction

Sexual cannibalism typically involves a female devouring a conspecific male immediately before, during or immediately after copulation. Although sexual cannibalism has been observed in a wide variety of predatory invertebrates, the majority of evidence comes from studies involving spiders or mantids (Elgar, 1992). To date, research into sexual cannibalism has largely focussed on discovering its adaptive function. Currently, there are three main hypotheses that suggest why sexual cannibalism is maintained in nature: (1) adaptive foraging—females devour males in order to gain essential nutrients and are more likely to do so when starved (Barry, Holwell, & Herberstein, 2008; Hurd et al., 1994; Roggenbuck, Pekár, & Schneider, 2011); (2) mate choice—sexual cannibalism represents an extreme form of mate choice in which non-preferred males are devoured to prevent copulation (Elgar, Schneider, & Herberstein, 2000; Hebets, 2003; Persons & Uetz, 2005; for a review see: Prenter, MacNeil, & Elwood, 2006); (3) aggressive spillover—adult female aggression towards conspecific males is a by-product of strong selection for juvenile aggression (Arnqvist, 1992; Henriksson, 1997; Johnson & Sih, 2005).

The extent to which females cannibalise males can vary greatly between individuals, species and taxonomic groups. For example, female *Dolomedes triton* (six-spotted fishing spider) show individually consistent differences in how likely they are to cannibalise males (Johnson & Sih, 2005). Female diet can create large variation in sexual cannibalism rates within species; female *Pseudomantis albofimbriata* (false garden mantis) cannibalise males at an average of 89% of encounters when starved, compared to 0% of encounters when satiated (Barry et al., 2008). Female attack rates in *Miomantis caffra* (springbok mantis) are not significantly affected by diet, with females cannibalising males at an average rate of 61% (Walker & Holwell, 2015). A field study on *Mantis religiosa* (the European mantis) indicates that females cannibalise males in only 31% of encounters (Lawrence, 1992). As well as variation in the overall rate of sexual cannibalism, variation in the probability of

cannibalism occurring before or after copulation also differs between species. For example, female free-living hunting spiders are known for their high tendency to attack males prior to copulation (see: Persons & Uetz, 2005 [wolf spiders] and Arnqvist, 1992; Johnson & Sih, 2005 [fishing spiders]). Conversely, females of some web-dwelling spiders typically wait until after copulation before attempting to devour the male (Forster, 1992; Herberstein, Schneider, & Elgar, 2002; Schneider & Lesmono, 2009).

Although the costs and benefits of sexual cannibalism for the individuals of a species have been thoroughly investigated (Barry et al., 2008; Brown & Barry, 2016; Newman & Elgar, 1991; Schneider & Elgar, 2001; Schwartz, Wagner, & Hebets, 2016), there are very few studies that attempt to address the population-level consequences of sexual cannibalism. There are two main negative effects that sexual cannibalism may have on population ecology. First, in all instances of sexual cannibalism, an adult male is removed from the population, which over time will deplete the availability of reproductive males in the population (Hurd et al., 1994; Lawrence, 1992). Second, in the case of pre-copulatory cannibalism, an adult male is removed from the population and both the male and the female miss out on copulation and the fertilisation of the female's eggs. Both of these effects of sexual cannibalism are likely to increase the proportion of adults in the population, both male and female, that die as virgins. As a result of high virgin death rates, the population may be more vulnerable to ecological decline via mechanisms such as reduced population growth rate (r) (Anthony & Blumstein, 2000; Miller et al., 2009).

Understanding the effects of individual behaviour on species ecology is important for determining population viability (Anthony & Blumstein, 2000; Blumstein, 1998). Here, we provide a theoretical framework that examines the potential effect of sexual cannibalism on population growth rate and population extinction risk. We also compare the population-

level effects of pre- and post-copulatory cannibalism separately to give a more holistic overview of how sexual cannibalism can impact on species ecology.

Methods

For robustness, we used two separate modelling approaches to address our central question of how sexual cannibalism affects population viability. We first programmed a discrete-time mathematical model. Mathematical models are noted for their conciseness and ability to generalise theoretical findings for a multitude of biological systems; however, for tractability they often ignore stochasticity that can be generated by natural variation. As such, we also constructed an individual-based model (IBM). IBMs consider individuals as discrete entities and incorporate uncertainty into a model. Due to the fact that system-specific behaviours are explicitly defined in IBMs, they are often seen as being more realistic relative to other types of theoretical model (Grimm, 1999). Both models were run in R version 3.4.3 (R Core Team, 2017). Code for both models is available at datadryad (doi:10.5061/dryad.gr5hc09).

Mathematical model

Our mathematical model is spatially implicit and assumes no migration of individuals. We assume males (M) search for mates continually until they are eaten by a female or reach their maximum mating quota (h). Males are always successful at finding a mate; we justify this assumption in sexually cannibalistic systems using the fact that, due to sexual cannibalism, adult death rates are likely to be greater for males than for females. As such, this will reduce the probability of sexually receptive females becoming scarce in relation to males; thus a significant reduction in male mate-finding rate is unlikely to occur. We assume an initial 1:1 adult sex ratio, based on Fisher's principle, and supported by field data from two sexually cannibalistic species (Arnqvist & Henriksson, 1997; Lawrence, 1992). Because our model considers a closed population (migration rate = 0) and assumes an even adult sex ratio, we can regard the average overall mating rate for males and females as

equal in a generation (i.e., if the average number of matings per male is two, then the average number of matings per female must also be two).

We gave h a constant value of 2, this value is in concordance with evidence from empirical studies, which suggest that the maximum number of lifetime matings for males in cannibalistic species is often two (Fromhage & Schneider, 2006; Herberstein, Gaskett, Schneider, Vella, & Elgar, 2005). In addition, we provide figures displaying how our model output is affected by varying the value of h in the Supporting Information. The probability of both pre-copulatory cannibalism (c_1) and post-copulatory cannibalism (c_2) was given separate values so that the ecological significance of both pre- and post-copulatory cannibalism could be investigated independently. After locating a female, there was probability k that the male would have the opportunity to mate. For the figures presented in the main manuscript k is kept at a constant value of 1, however figures displaying how our results are affected by varying k are provided in the Supporting Information. The total number of matings that have taken place over the breeding season, m, is therefore given by

$$m = kM(1 - c_1)\left(1 + \sum_{j=1}^{h-1}\{(1 - c_1)(1 - c_2)\}^j\right).$$

(1)

Since the female population is not explicitly defined in the mathematical model, fecundity was quantified in terms of the number of males produced per mating over the course of a breeding season. The minimum number of males produced per copulation was defined as a. Fecundity benefits (b) could be gained from both pre-copulatory cannibalism and post-copulatory cannibalism. The cannibalism derived fecundity benefits were assumed to increase linearly with the probability of sexual cannibalism occurring. As there is no conclusive evidence to state that either pre- or post-copulatory cannibalism has a greater

potential to increase female fecundity, we assume that both cannibalism rates influence

fecundity equally. As such, the mean number of males produced per copulation is

$$f = (a + bac_1 + bac_2).$$

(2)

Therefore, the mean N_{t+1} is

$$N_{t+1} = mf = kM(1 - c_1)\left(1 + \sum_{j=1}^{h-1}\{(1 - c_1)(1 - c_2)\}^j\right)(a + bac_1 + bac_2).$$

(3)

Stochastic model

A stochastic individual-based model, running on a daily cycle, was also used to simulate the

lifecycle of a sexually cannibalistic system. Each day, males and females had a constant

probability γ of dying via a means other than sexual cannibalism. Individual males were

then given the opportunity to find a mate. The probability L_m of finding a mate was

assumed to have a hyperbolic relationship with the number of receptive females present in

the population. There is evidence for hyperbolic resource-finding relationships in other

arthropod species (Hassell, Lawton, & Beddington, 1976). As such, male mate location

probability was defined as

$$Lm = \frac{h\left(\frac{R_t}{R_t + \theta}\right)}{\delta},$$

(4)

where δ denotes total breeding season length (days), R_t is the number of receptive females

at time *t*, *h* is the maximum number of matings a male can achieve in his lifetime and θ is a

constant used to determine the gradient of the mate-finding curve. Females were assumed

to become non-receptive once mated; however, after a gestation period (μ) they became

receptive again so that when *t* > μ,

$$R_t = F_t - m_{tot(t)} + m_{t-\mu},$$

<div align="right">(5)</div>

where F_t is the total number of females at time t, $m_{tot(t)}$ is the total number of matings that

had taken place up until time t, and $m_{t-\mu}$ is the number of matings that took place at time

$t - \mu$. After locating a mate, males can be cannibalised before copulation with probability

$L_{m1} = L_m c_1$, copulate successfully with probability $L_{m2} = L_m(1 - c_1)$, copulate and then be

cannibalised with probability $L_{m3} = L_{m2} c_2$, or copulate and then survive with probability

$L_{m4} = L_{m2}(1 - c_2)$. The probabilities of the aforementioned events occurring were then used

to create a multinomial random number vector containing the number of males that were

assigned to each event. The simulation ran for a series of δ days, and the number of

successful mating events that occurred throughout the season was summed to give m.

Average female fecundity (f) was defined in the same way as for the mathematical model

(Equation 2). Values for f were varied following a Poisson distribution to imitate natural

variation in female fecundity. The number of adults present at N_{t+1} is then calculated by

mf. Population growth rate is then calculated by N_{t+1}/N_t. To minimise any influence that

initial population size may have on population growth rate, the above process was

repeated for a range of initial population sizes to determine a reliable mean value for

population growth rate.

Results

Please note: the absolute values for population growth rate produced by these models are

sensitive to initial parameter values. Because initial parameter settings cannot be made

appropriate for all of the species that the model is relevant to, any conclusions drawn from

absolute values would be unreliable. As such, the y-axis in this section is often not fully

labelled. Code for the models is available at datadryad.org for production of results for

specific initial parameter values.

Sexual cannibalism causes adult male deaths and, in some cases, leads to both the male and female missing out on copulation. Our models show that an overall increase in sexual cannibalism leads to consistently lower mating rates (Figure 1). This was true for both the mathematical model and the stochastic model. Although this result is unsurprising, it is a necessary premise to support our further findings.
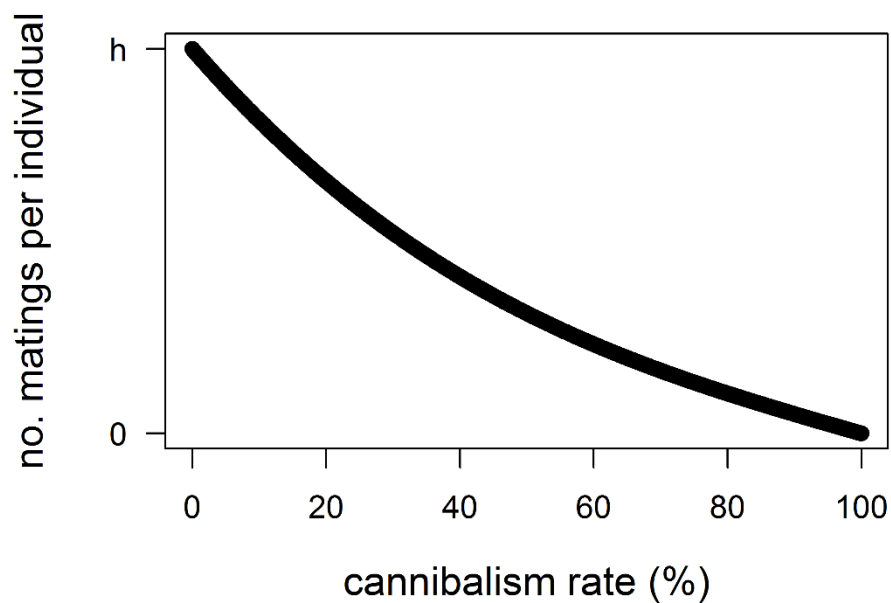
Figure 1 - The average number of matings per individual declines in response to increasing sexual cannibalism rate. Here, it is assumed that pre- and post-copulatory cannibalism rates are equal. *h* is the average maximum number of lifetime matings per individual.

Sexual cannibalism and population growth rate

Our mathematical and stochastic model showed very similar trends for the effect of sexual cannibalism on population growth rate (Figure 2), both in the presence and in the absence of cannibalism-derived fecundity benefits (*b*). In the absence of any type of fecundity benefit (*b* = 0), sexual cannibalism consistently decreases population growth rate. However, in the presence of fecundity benefits, sexual cannibalism can increase population growth rate, with increased fecundity benefits causing higher growth rates across all rates of sexual

cannibalism (Figure 2a). Increasing the value of *b* caused a type II functional response in the

rate of sexual cannibalism that gave the highest growth rate value (Figure 2b), that is, the

rate of increase in the optimal cannibalism rate for population growth decreases as *b*

becomes larger. The highest optimum cannibalism rate was 36% for the mathematical

model and 43% for the stochastic model.
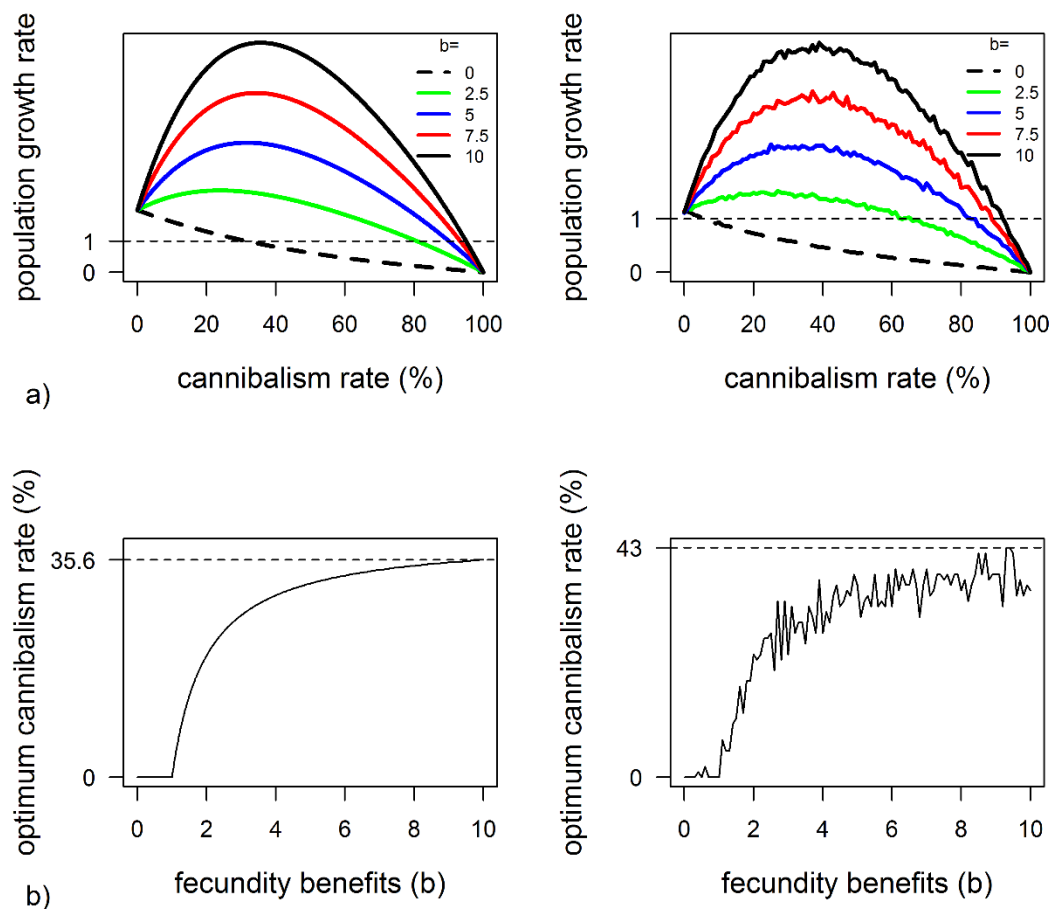
Figure 2 - (a) Variation in population growth rate in response to cannibalism rate and the fecundity benefits of sexual cannibalism (*b*). The horizontal dashed line represents the extinction threshold. (b) Variation in optimum cannibalism rate for population growth in response to increased *b* value. Pre- and post-copulatory cannibalism rates are assumed to be equal for these illustrative results. Results from the mathematical model are displayed on the left, IBM results on the right.

Higher rates of sexual cannibalism caused population growth rate to decline and eventually

fall below the extinction threshold, below which the population is expected to decline in

size each generation (Figure 2a). Lower *b* values caused the curves to fall below the

extinction threshold sooner than curves representing higher *b* values. For example, when

b = 0, the mathematical model predicted that a population would go extinct when the rate

of sexual cannibalism is >32%. The individual-based model predicted a threshold of >6%

when *b* = 0. However, when a positive *b* value was used (*b* ≥ 2.5), populations would not go

extinct until cannibalism rates became >82% in the mathematical model and >66% in the

stochastic model.

Pre- versus post-copulatory cannibalism

When observed separately, pre- and post-copulatory had different effects on population

growth rate (Figure 3a, b). Results from both the mathematical model and the IBM showed

that pre-copulatory cannibalism had a largely negative effect on population growth rate

(Figure 3a). The mathematical model and the IBM showed a consistent decrease in

population growth rate in response to an increase in pre-copulatory cannibalism rate. Both

models show that changes in post-copulatory cannibalism rate have only a small effect on

population growth rate, and that this effect decreases as pre-copulatory cannibalism rate

increases (i.e., the separate lines merge, Figure 3a). Both the mathematical model and the

IBM show that post-copulatory sexual cannibalism consistently increases population

growth rate (Figure 3b). In both models, higher pre-copulatory cannibalism rates led to

consistently lower growth rates (Figure 3b).
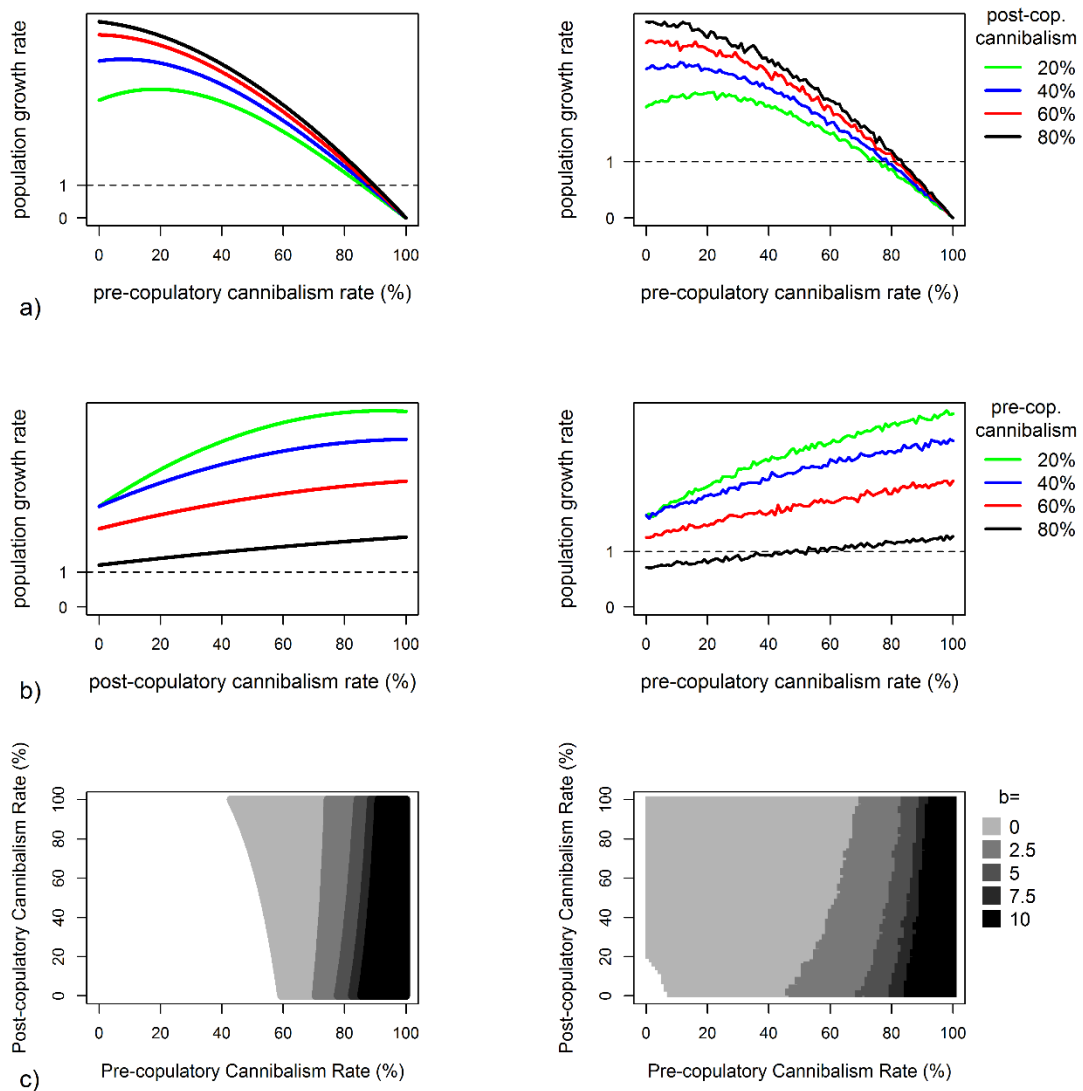
Figure 3 - (a, b) Variation in population growth rate in response to changes in both pre- and post-copulatory cannibalism rate (b = 5). In Figure 3a, pre-copulatory cannibalism rate is on a continuous scale while each individual line represents a fixed value for post-copulatory cannibalism rate. For Figure 3b, post-copulatory cannibalism rate is varied whilst pre-copulatory cannibalism rate is fixed. (c) Effect of pre- and post-copulatory cannibalism rate and the amount of cannibalism derived benefits (b) on population extinction zone (shaded areas). Results from the mathematical model are displayed on the left, IBM results on the right.

Whether the population was able to remain above the extinction threshold was largely determined by the rate of pre-copulatory sexual cannibalism, with post-copulatory cannibalism having only a small effect (Figure 3c). This was true for both the mathematical and IBM. In the presence of a positive b value ($b \geq 2.5$), extinction only occurred at intermediate to high rates of pre-copulatory sexual cannibalism. A pre-copulatory

cannibalism rate of >75% would cause a population to go extinct in the mathematical model, in the IBM a pre-copulatory cannibalism rate of >≈ 48% would cause population extinction. Removing the fecundity benefits of sexual cannibalism ($b = 0$) sees the extinction threshold shift so that lower rates of pre-copulatory cannibalism can cause extinction, even when post-copulatory cannibalism rates are low. This was particularly true of the IBM in which only very low values of pre- and post-copulatory cannibalism did not cause population extinction. A b value of zero also saw the effect of post-copulatory cannibalism on population growth rate change from positive to negative (Figure 3c).

Discussion

Using theoretical models, we have demonstrated that sexual cannibalism can have both positive and negative impacts on population growth rate. Intermediate rates of sexual cannibalism give the highest population growth rate (r) values when cannibalism-derived fecundity benefits (b) are present. This finding is likely to represent a behavioural trade-off in which nutrients gained from intermediate cannibalism rates lead to a higher rate of offspring production, despite cannibalism reducing the number of matings taking place in the population. However, we have also shown that high rates of sexual cannibalism can reduce population growth below the replacement rate, potentially leading to population extinction, particularly when the fecundity benefit of cannibalism is low. Pre-copulatory cannibalism was far more likely to reduce population growth rate than post-copulatory cannibalism. Our IBM generated lower absolute values for population growth rate than the mathematical model, this was likely due to female supply being limited in the IBM but not in the mathematical model. However, the overall trends produced were very similar for both models.

When does sexual cannibalism increase the productivity of a population?
Unsurprisingly, if cannibalism does not improve female fecundity, cannibalism always lowers population growth (Figure 2). Thus, fecundity benefits make it more likely for

sexually cannibalistic mating systems to persist in nature. There is substantial evidence that sexual cannibalism increases lifetime fecundity for the female, and sometimes the male (Andrade, 2003; Brown & Barry, 2016). Often this is thought to occur through increased egg production owing to extra nutrients derived from the cannibalised male (Brown & Barry, 2016; Spence, Zimmermann, & Wojcicki, 1996). For example, female *Pseudomantis albofimbriata* that cannibalise males are known to increase their ootheca mass by up to 40% when compared to females that do not cannibalise (Barry et al., 2008). More recently, it was shown that female dark fishing spiders (*Dolomedes tenebrosus*) that cannibalised males produced twice as many offspring as females that did not cannibalise or were given an alternative post-copulatory meal (Schwartz et al., 2016).

Another way in which sexual cannibalism may increase individual fecundity is via improved offspring quality (Berning et al., 2012; Pruitt et al., 2014). There is evidence that in some species sexual cannibalism is used as a method of mate choice (for a review see: Prenter et al., 2006); as such, cannibalistic females may be able to mate with higher quality males and produce offspring that are more viable. In both *Schizocosa ocreata* (wolf spiders) and *Araneus diadematus* (garden-orb spiders), females are more likely to exhibit pre-copulatory cannibalism on males that are relatively small (Persons & Uetz, 2005). Similarly, in the fishing spider *Dolomedes fimbriatus*, larger males are more likely to evade pre-copulatory cannibalism attempts by females and are therefore more likely to copulate (Arnqvist, 1992; Kralj-Fišer et al., 2016). Sexual cannibalism may also improve offspring viability indirectly through aggressive spillover, in which sexually cannibalistic behaviour is linked to greater feeding voracity as a juvenile, which in turn leads to higher juvenile survival (Arnqvist, 1992; Henriksson, 1997; Johnson & Sih, 2005). As such, sexually cannibalistic adults may produce more voracious offspring that survive better. Both increased egg production and improved offspring quality represent mechanisms by which sexual cannibalism can be beneficial for individuals.

Our results suggest that intermediate rates of sexual cannibalism yield the highest population growth rates when pre- and post-copulatory cannibalism rates are equal (Figure 2a: 24%–26% in the mathematical model, 18%–52% in the IBM). Evidence from field and laboratory studies suggest that cannibalism rates often fall into this intermediate range. In the wild, European mantis (*Mantis religiosa*) females cannibalised potential mates in 31% of encounters (Lawrence, 1992), with similar rates seen in other mantids (*Hierodula membranacea*, Birkhead, Lee, & Young, 1988; *T. sinensis*, Lelito & Brown, 2006). Evidence from studies involving spiders also demonstrates a tendency for females to cannibalise males at an intermediate rate (*Nephila plumipes*, 56%–61% in Schneider & Elgar, 2001; *D. triton*, 21%–53% in Johnson, 2001). It may be that intermediate levels of sexual cannibalism represent an optimal trade-off between reduced mating rate and increased reproductive output per mating, and are thus selected for at the individual level. Alternatively, it could be that species or populations in which high levels of sexual cannibalism are selected for at the individual level are indeed at a higher risk of extinction and so do not persist.

Our results show that even high rates of post-copulatory cannibalism are not detrimental to population growth when cannibalism provides fecundity benefits (Figure 3b). Post-copulatory cannibalism may represent the "best of both worlds" for females in terms of reproductive output, as it allows the female to secure a mate and potentially increase egg production through devouring the male. In some species, strict post-copulatory cannibalism is apparent, with females devouring the male before copulation only in rare cases. For example, female orb-web spiders of the genus *Argiope* typically only attack the male after he has successfully mounted (Schneider & Lesmono, 2009). Although post-copulatory cannibalism has the potential to reduce the lifetime number of matings for males, males of some species are complicit in being devoured by the female after copulation has taken place, including the redback spider (*Latrodectus hassellti*) (Andrade,

2003), the dark fishing spider (*Dolomedes tenebrosus*) (Schwartz et al., 2016) and the wasp spider (*Argiope bruennichi*) (Fromhage, Uhl, & Schneider, 2003). It is theorised that the increase in paternal output the male receives by allowing himself to be eaten by the female offsets the cost of reducing his lifetime number of matings (Buskirk, Frohlich, & Ross, 1984).

When is sexual cannibalism likely to be detrimental to population survival?
Our models indicate that scenarios in which pre- and post-copulatory sexual cannibalism rates are high can lead to low population growth (Figure 2a) and potentially lead to population extinction (Figures 2a and 3c), even if the fecundity benefits of cannibalism are high. As such, it would seem unlikely that populations in which individuals demonstrate such high cannibalism rates would persist in nature. However, environmental conditions can substantially increase cannibalism rates. Laboratory studies have found tenfold increases in cannibalism rates when females are starved (*Hierodula membranacea*: Birkhead et al., 1988; *Stagmomantis limbata:* Maxwell, Gallego, & Barry, 2010), suggesting that females in poor-quality habitats, where nutrients are scarce, would cannibalise more frequently. Rates of sexual cannibalism may also increase if there is a decrease in male quality in systems where sexual cannibalism acts as mate selection in which females cannibalise unattractive males (Arnqvist, 1992; Persons & Uetz, 2005). For example, in the wolf spider *Hogna helluo* rates of sexual cannibalism rate can increase from 0% to 80% as male size relative to the female decreases (Wilder & Rypstra, 2008). Therefore, if males that develop in poor-quality habitats do not grow to an adequate size, sexual cannibalism rates may become elevated.

Sexual cannibalism is more likely to reduce population growth below the replacement rate when fecundity benefits are low (Figures 2a and 3c). Hence, the ecological viability of a cannibalistic population may be highly dependent on the nutritional value of males. It is possible that males that develop in poor-quality habitats are less nutritious and therefore

provide less of a fecundity benefit for females. As of yet there are no studies that test this theory. Further experimental investigation into how environmental factors affect male nutritional value quality is needed in order to establish a link between habitat quality and the population-level effects of sexual cannibalism.

Pre-copulatory cannibalism was shown to be largely detrimental for population growth rate (Figure 3a). An increase in a female's tendency to cannibalise males before copulation may therefore be detrimental for population growth rate. Although there is little evidence on whether local conditions can increase pre-copulatory cannibalism in nature, a recent paper has shown that pre-copulatory cannibalism rates in female wolf spiders increased significantly in response to feeding regime and relative male size in the laboratory (Gavín-Centol, Kralj-Fišer, De Mas, Ruiz-Lupión, & Moya-Laraño, 2017). Alternatively, if sexual cannibalism occurs due to spillover of juvenile aggression, then poor habitats may select for highly aggressive juveniles (Johnson & Sih, 2005), thereby increasing the rate of adult cannibalism. Thus, if reducing habitat quality does in fact increase female hunger and reduce male size, then not only may we see an increase in cannibalism rate overall, but specifically an increase in pre-copulatory cannibalism, with potentially greater impacts on population viability.

In summary, our models suggest that populations may suffer increased extinction risk when (1) cannibalism rates are high, (2) fecundity benefits of cannibalism are low, and (3) there is a shift from post-copulatory to pre-copulatory cannibalism. There are reasons to believe all three processes are likely to occur when habitat quality is declining. This may make sexually cannibalistic species particularly vulnerable to environmental change.
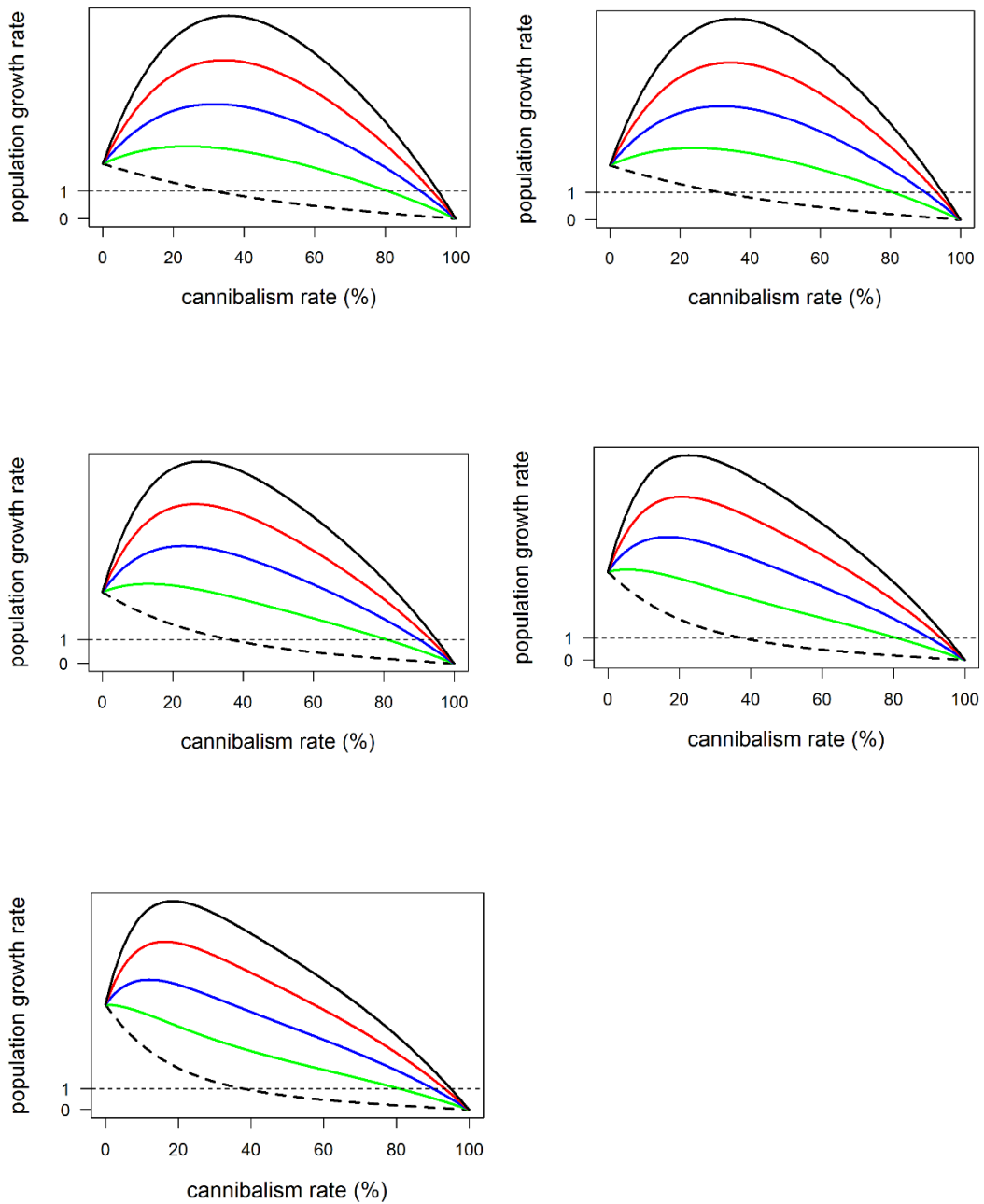
Figure S1 – Variation in population growth rate in response to cannibalism rate and cannibalism induced fecundity benefits when the maximum number of matings a male can achieve in is life time (h) is 1 (top left), 2 (top right), 3 (mid left), 4 (mid right) and 5 (bottom left).
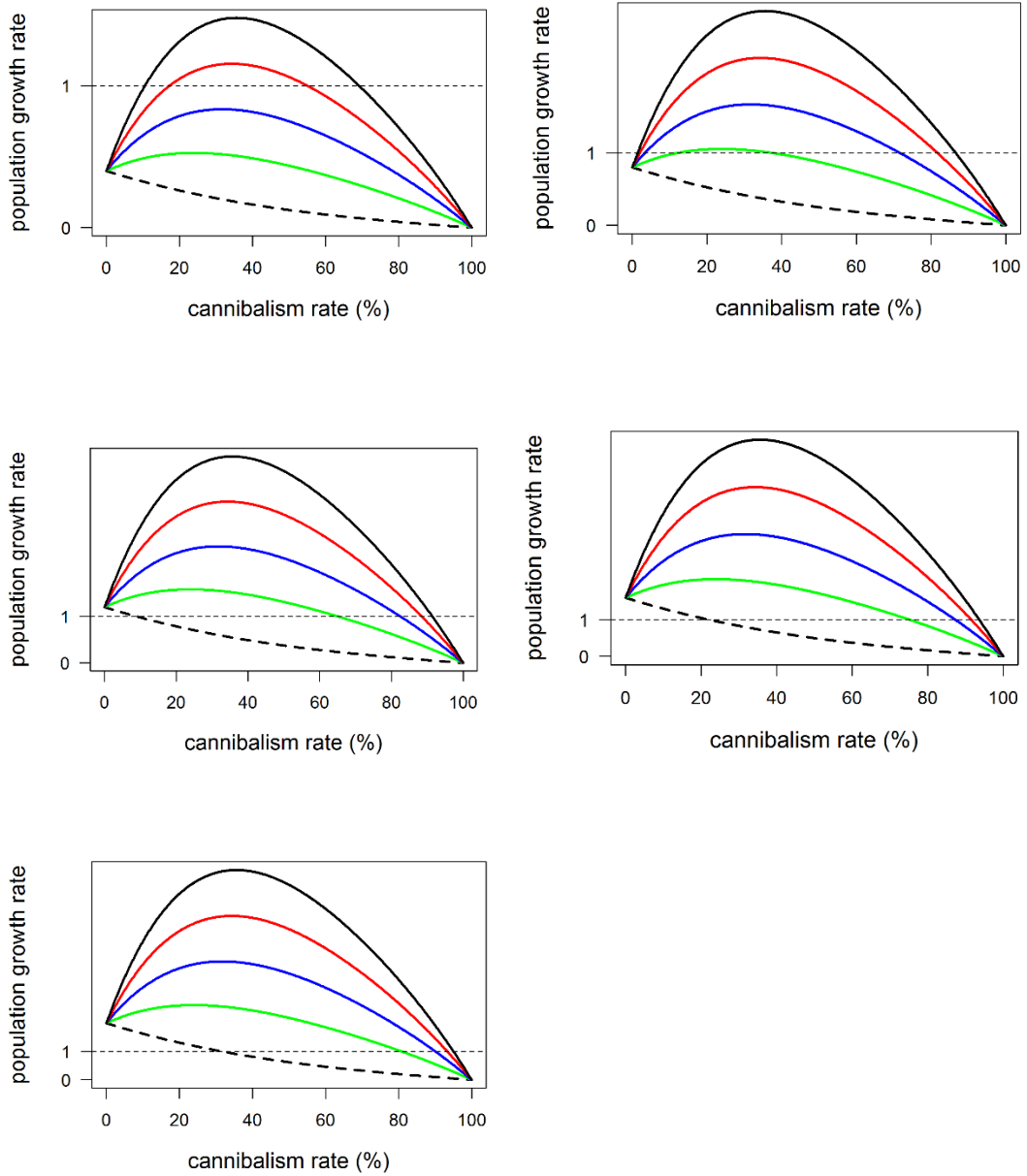
Figure S2 – Variation in population growth rate in response to cannibalism rate and cannibalism induced fecundity benefits when the probability a male that has located a female will attempt to mate is 0.2 (top left), 0.4 (top right), 0.6 (mid left), 0.8 (mid right) and 1 (bottom left).

CHAPTER 2: Mate-finding Allee effects can be exacerbated or relieved by sexual cannibalism

Abstract

Allee effects occur when individual or population survival decreases due to populations being small or sparse. A key mechanism underlying Allee effects is difficulty in finding mates at low densities. Species may be particularly vulnerable to mate-finding Allee effects if females rely on an abundance of males to reproduce successfully. In sexually cannibalistic species, females may consume males before or after copulation, potentially reducing the supply of males to the point where a mate-finding Allee effect occurs. In this study, we investigate the extent to which sexual cannibalism can drive Allee effects, and the conditions under which sexual cannibalism is likely to be particularly detrimental to population viability. We created an individual-based model that tracked specific females throughout the breeding season and used extinction risk and per capita growth rate to measure the strength of the Allee effects. We varied both founder population size and mate encounter rate independently of each other to expose the mechanism driving the Allee effects. We also analysed how cannibalism-derived female fecundity benefits affected extinction risk. We found that sexual cannibalism could lead to high extinction risk, particularly when cannibalism occurred before copulation, founder population size was small, and mate encounter rates were low. However, post-copulatory cannibalism reduced extinction risk, if cannibalism increased female fecundity enough. We found that there were strong threshold effects, in which small changes in encounter rate could strongly alter population extinction risk. We find that sexual cannibalism is likely to negatively impact population survival as population size and mate encounter rate decrease. This may be exacerbated if male quality declines and female hunger increases in declining populations. As many top invertebrate predators, such as spiders and mantids are sexually cannibalistic, this may have ecosystem-wide impacts. We also suggest that other reproductive

behaviours, such as rejecting all but high quality mates or requiring multiple mates to ensure fertility, are also likely to cause mate-finding Allee effects when habitat quality degrades.

Introduction

Anthropogenically imposed disturbance to habitats often leads to rapid reductions in the size and density of natural populations. Allee effects occur when individual fitness and/or population viability suffers as a result of a population being too small or sparse (Odum & Allee, 1954; Stephens & Sutherland, 1999). Species differ in how vulnerable they are to Allee effects; some species may be naturally rare or have experienced rapid population declines in their recent evolutionary past, making them better adapted to living in small or sparse populations (Sih, Ferrari & Harris 2011). However, other species may have evolved under high densities and need high numbers of neighbouring conspecifics for successful survival and reproduction (Courchamp, 1999). For instance, several species of communally breeding birds rely on conspecifics to help with the feeding, grooming and warming of offspring; as a result, a reduction in group size can lead to a reduction in offspring survival (Courchamp, 2000). In other species, individuals rely on conspecifics for predator detection or deterrence and may suffer from increased predation risk when population size is reduced (Heinsohn, 1992; Clutton-Brock, 1999; Wittmer, Sinclair & McLellan 2005; Cunha, Fontenelle & Griesser 2017). For example, population declines in the once near-extinct Californian island fox (*Urocyon littoralis*) have been partly attributed to increased predation by golden eagles (*Aquila chrysaetos*) at low population sizes (Angulo, Roemer, Berec, Gascoigne & Courchamp 2007).

One of the most commonly reported mechanisms by which Allee effects can impact animal populations is an increased difficulty in finding suitable mates as populations become small or sparse; this is known as the "mate-finding" Allee effect (Wells, Strauss, Rutter & Wells 1998). Mate-finding Allee effects can have negative consequences for both individuals and

populations, with theoretical models and empirical data predicting that species with restricted dispersal ability are most at risk (Dobson & Lees, 1989; Takasu, 2009; Rhainds, 2019). For example, female gypsy moths (*Lymantria dispar*) have a lower probability of mating at lower population densities due to males having an increased difficulty in finding a mate (Tcheslavskaia, Brewster & Sharov 2002; Johnson, Liebold, Tobin & Bjørnstad 2006). Conversely, some species can maintain mate-encounter rates at low densities. Kindvall, Vessby, Berggren & Hartman (1998) showed that mating rates in Roesel's bush cricket (*Metrioptera roseli*) can be maintained at low densities through increased movement of individuals. Whilst individuals of some species can counteract the effects of increased mate scarcity by increasing their mate-finding effort, there remains an array of species from various taxa where individuals suffer reductions in fitness due to mate scarcity (Gascoigne, Berec, Gregory & Courchamp 2009). In some scenarios, greater dispersal rates or distances may be inadequate or negative for protecting individuals or populations from Allee effects (Shaw & Kokko, 2014). For example, the dispersal rates of male Granville fritillary butterflies (*Melitaea cinxia*) increase in small populations, exacerbating demographic Allee effects by further reducing population size and distorting the sex ratio leading to a reduced per capita growth rate (Kuussaarim Saccheri, Camara & Hanski 1998). Moreover, this illustrates how populations in which individuals attempt to counteract Allee effects by increasing their dispersal rate may suffer negative demographic effects due to fitness trade-offs (Berec, Kramer, Bernhauerová & Drake 2018).

Some mating behaviours have evolved such that females require access to a large number of potential mates in order to thrive, and these may make species particularly vulnerable to mate-finding Allee effects. For example, in species where male sterility is particularly prevalent, females are required to mate with multiple males to ensure they become fertilised (García-González, 2004). Species in which females regularly reject potential mates based on perceived fitness (Blanckenhorn, Mühlhäuser, Morf, Reusch & Reuter 2000;

Persons & Uetz, 2005) may see a dramatic increase in virgin death rates if mate availability decreases with population size or density but female choosiness persists (Møller & Legendare, 2001). Populations that exhibit sexual cannibalism, in which individuals eat potential mates, could also be at an increased risk of suffering from Allee effects due to the active removal of reproductive males from the population leading to a reduction in the number of successful copulations in the population (Fisher, Cornell, Holwell & Price 2018).

Sexual cannibalism has been reported in many species of predatory invertebrate, including those in keystone groups such as spiders, and usually occurs when a female devours a male prior to, during, or immediately after copulation (Spiders: Schneider & Elgar, 2001; Johnson & Sih, 2005; Persons & Uetz, 2005, Mantids: Lawrence, 1992; Walker & Holwell, 2015). Sexual cannibalism can benefit females (and occasionally males, see Andrade, 1996) by increasing egg production (Schwartz, Wagner & Hebets 2016), preventing matings with unsuitable males (Prenter, MacNeil & Elwood 2006), and increasing juvenile foraging voracity (Arnqvist & Henriksson, 1997). However, sexual cannibalism can also be costly for individual fitness and population viability under some ecological scenarios (Buskirk, Frolich & Ross 1984; Fisher, Cornell, Holwell & Price 2018). In all instances of sexual cannibalism, a reproductive male is removed from the population, and in the case of pre-copulatory cannibalism both the male and female miss out on copulation, potentially increasing the incidence of females dying without ever mating. At low population densities, when encounters with potential mates are rare, females may be more likely to cannibalise all of the males they encounter. Similarly, in small populations, the frequency of sexual cannibalism may fluctuate greatly due to increased stochasticity in the number of cannibalistic individuals (Dennis, 2002), potentially leading to a scenario in which cannibalism is frequent enough to cause extinction. In the current study, we used stochastic simulation modelling to provide the first insights into the relationship between sexual cannibalism and extinction risk in small or sparse populations. We predicted that the

likelihood of demographic Allee effects occurring would increase with the rate of sexual cannibalism.

Methods

We used a spatially implicit individual-based model broadly based on the lifecycle of a dioecious sexually cannibalistic invertebrate. The model ran on a daily cycle (each timestep t representing one day) of δ days per season. The model tracked the status of females throughout the breeding season. Because the past status of males was not relevant to our questions, individual males were not defined. At the end of each breeding season individuals died off, meaning that generations did not overlap. An initial sex ratio of 50:50 was assumed. At the beginning of each day all individuals had a 0.5% probability of dying such that $I_{t+1} \sim Bin(I_t, \lambda)$, where I_t is the number of individuals alive at the end of time-step t and $\lambda = 0.995$ is the proportion of individuals that survive to the next time-step (excluding male deaths caused by cannibalism). Surviving males then had the opportunity to locate a receptive female. The probability that a female would be successfully located by a male was given a hyperbolic relationship with the number of males present in the population (Fig. 1). This follows evidence for hyperbolic resource-finding relationships in arthropod species (Hassell, Lawton & Beddington 1976). Thus probability that a male located a female at timestep t was set to

$$p_t = \frac{h}{\delta}\left(\frac{M_t}{M_t + \theta}\right),$$

Equation 1

where M_t is the number of males present in the population at time t, θ is a positive constant used to define the gradient of the mate-finding curve, and h is a parameter that controls the average number of matings per male. If the number of males is large ($M_t \gg \theta$), then $\frac{M_t}{M_t + \theta} \approx 1$ and, over the season, the mean number of males a female will encounter

will be $p_t\delta \approx h$ females. Note that we must have $h < \delta$ to ensure $p_t < 1$, and we choose

$h = 2$ following evidence from various cannibalistic species (Herberstein, 2005; Fromhage

& Schneider, 2006). Hence whether or not each female met a male during timestep t was

determined by $\sim Bin(1, p_t)$. The mean probability that a female would cannibalise a male

before or after copulation is denoted as c_1 and c_2 respectively. A uniformly generated

pseudorandom number was used to determine whether a female that had been located by

a male would cannibalise the male prior to copulation (probability c_1), cannibalise after

copulation (probability $(1 - c_1)c_2$), or copulate and not cannibalise (probability

$((1 - c_1)(1 - c_2))$. The outcome of the male-female encounter was then recorded. The

number of males in the population was reduced in accordance with the number of natural

deaths and instances of cannibalism that occurred. Females were assumed to become non-

receptive once mated; however, after a gestation period of $u = 42$ days females became

receptive once again.

The average number of offspring that survived to adulthood per copulation was $a = 2$, but

copulations in which females devoured males could yield additional fecundity benefits (b).

Fecundity benefits were gained if females devoured a male prior to copulation on a

previous day and had not mated since. Copulations in which females devoured males

immediately after copulation also yielded increased fitness benefits. At the end of each

season we summed the number of non-cannibalistic copulations (φ), copulations that were

preceded by pre-copulatory cannibalism (φ_{c1}), and instances of post-copulatory

cannibalism (φ_{c2}). We varied the number of offspring produced per copulation using a

Poisson distribution. As such, the total number of offspring produced under each of the

three copulatory scenarios was $\sum \sim Pois(\varphi\, a)$, $\sum \sim Pois(\varphi_{c1}(\, a + ab))$, and

$\sum \sim Pois(\varphi_{c2}(\, a + ab))$.

Table 1 – Model variables and parameters.

Parameter	Definition	Value(s)
δ	The number of days in a breeding season (the number of times the model was run per generation)	90
c_1	Probability of pre-copulatory cannibalism	0-1
c_2	Probability of post-copulatory cannibalism	0-1
λ	The average daily proportion of individuals that avoid natural deaths	0.995
I_t	The total number of individuals alive at time t (days)	Varies
R_t	The number of sexually receptive females alive at time t (days)	Varies
M_t	The number of males alive at time t (days)	Varies
h	The maximum number of matings a male can achieve in his lifetime	2
θ	A constant used to define the gradient of the mate-finding probability curve, higher values reduce the gradient	Varies
φ	The number of matings that occurred over the breeding season that were not affected by cannibalism	Varies
φ_{c1}	The number of matings over the breeding season that occurred after an incidence of pre-copulatory cannibalism	Varies
φ_{c2}	The number of matings over the breeding season in which cannibalism occurred immediately after	Varies
u	Female gestation period (days)	42
a	Mean number of offspring that survive to adulthood produced per copulation	2
b	Mean maximum increase in offspring that survive to adulthood as a result of sexual cannibalism	Varies

We measured the strength of an Allee effect using extinction probability and per capita growth rate (*r*). We defined the Allee threshold as when the probability of extinction was > 0.5. To calculate extinction probability, we ran 100 repeats of 10 generations of the model, the extinction probability was then simply the proportion of repeats in which the population went extinct. To calculate r, the model was run for two generations and r was defined as $\frac{N_{t+1}}{N_t}$. Evidence suggests that difficulty in finding a mate may be the most common cause of Allee effects in nature (Gascoine, Berec, Gregory & Courchamp 2009). As such, to simulate the effects of changes in founder population density or size, changes were made to the gradient of the mate-finding probability curve defined by equation 1. To

imitate variation in the density of the founder population, founder population size was kept

constant at 400 individuals whilst θ varied from 30-150. This had the effect of varying the

gradient of the mate-finding probability curve, where low gradients (high θ values)

corresponded to a relatively sparse population in which fewer male-female encounters

would take place for a given number of receptive females (Fig. 1, left). Under some

ecological scenarios it may be that population size, but not necessarily density, is reduced

as a result of anthropogenic disturbance. In order to manipulate population size whilst

controlling for first generation mate-encounter rate, smaller founder populations were

assigned steeper mate-finding probability curves (Fig. 1, right). To do this, θ had to vary

with respect to the initial number of receptive females present in the founder population

(R_0). By rearranging equation 1 for θ at $t = 0$ we get

$$\theta = R_0 \left(\frac{h}{p_0 \delta} - 1 \right)$$

Equation 2

where $p_0 \delta$ was given a constant initial value of 1.5. This method of defining θ was used

only when manipulating founder population size whilst controlling for density. All

simulations were run on R version 3.4.3 64-bit.
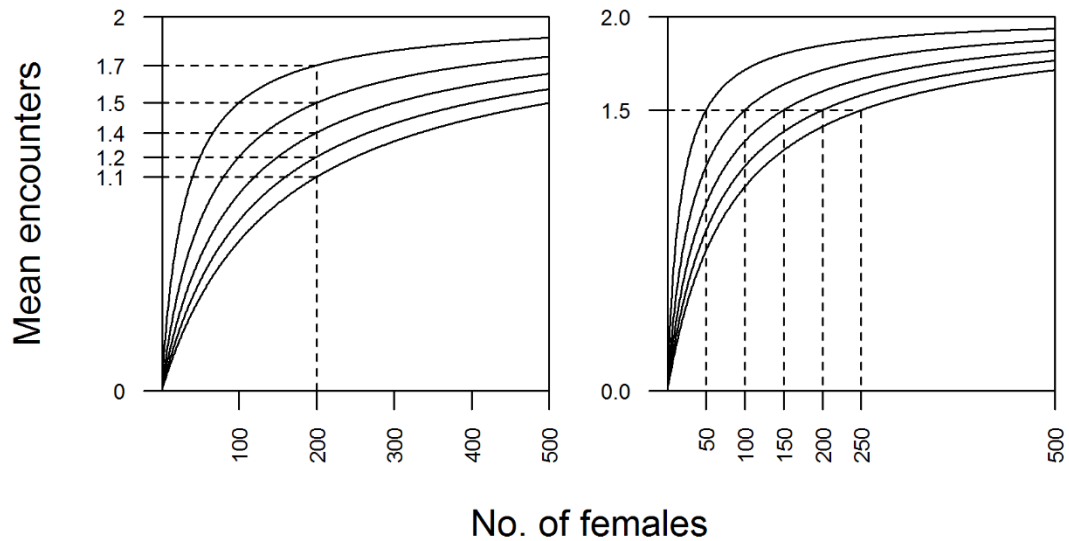
Figure 1 – Variation in the number of male-female encounters in response to the number of receptive females in the population. Where the dashed line intercepts the x-axis indicates founder population size, and where the dashed line crosses the y-axis indicates the mean total number of male-female encounters that occur in the first generation of a given population. On the left, founder population size remains constant as the mean number of encounters varies. On the right, founder population size varies while mean number of encounters remains constant. Founder population sizes and male-female mean encounter rate reflect the values that were used in the simulations presented in this paper.

Results

Intra-seasonal dynamics

Populations where males were devoured prior to copulation experienced fewer copulations throughout the breeding season (Fig. 2). The number of receptive females in the population decreased more rapidly in populations where cannibalism occurred after copulation. After the female gestation period, the number of receptive females began to increase. As expected, increasing the average mate encounter rate increased the average number of copulations that took place over the course of a breeding season.
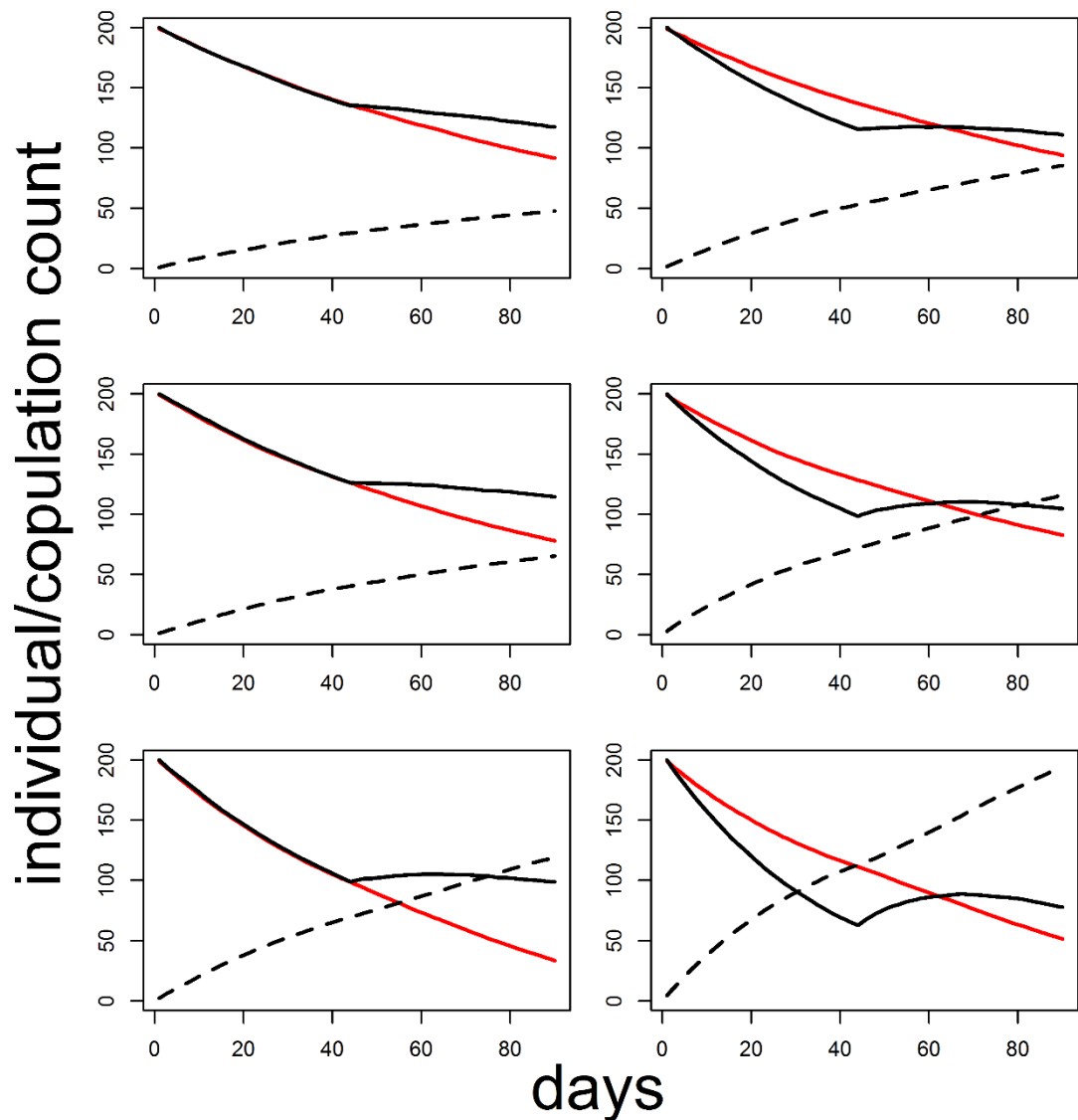
Figure 2 – Variation in the abundance of males (red), receptive females (black) and the cumulative copulation count (dashed) over the course of a breeding season in populations where females display either pre- (left-hand side) or post-copulatory (right-hand side) cannibalism. Cannibalism remained constant at 50% and mate encounter rate changed from 0.8 (top row), 1.1 (middle row), and 2 (bottom row).

Founder population size

When first generation mate encounter rate remained constant at 1.5, extinction probability was not sensitive to changes in founder population size among populations exhibiting pre-copulatory sexual cannibalism (Fig. 3, left). Increasing the founder population size reduced extinction probability in populations where the average pre-copulatory cannibalism rate

was 20 or 40%; this was true irrespective of whether pre-copulatory cannibalism could increase female fecundity by 0, 50 or 100%. As the potential for pre-copulatory cannibalism to increase female fecundity increased, extinction risk decreased more sharply with increasing population size. When the average pre-copulatory cannibalism rate in a population was >40%, extinction probability remained high, even the fecundity benefits of cannibalism were increased. In populations where females cannibalised males after copulation, extinction risk was only >0 when founder population size was very small. As such, extinction risk decreased rapidly as founder population size increased, and extinction risk was not noticeably affected by cannibalism rate (Fig. 3 right).
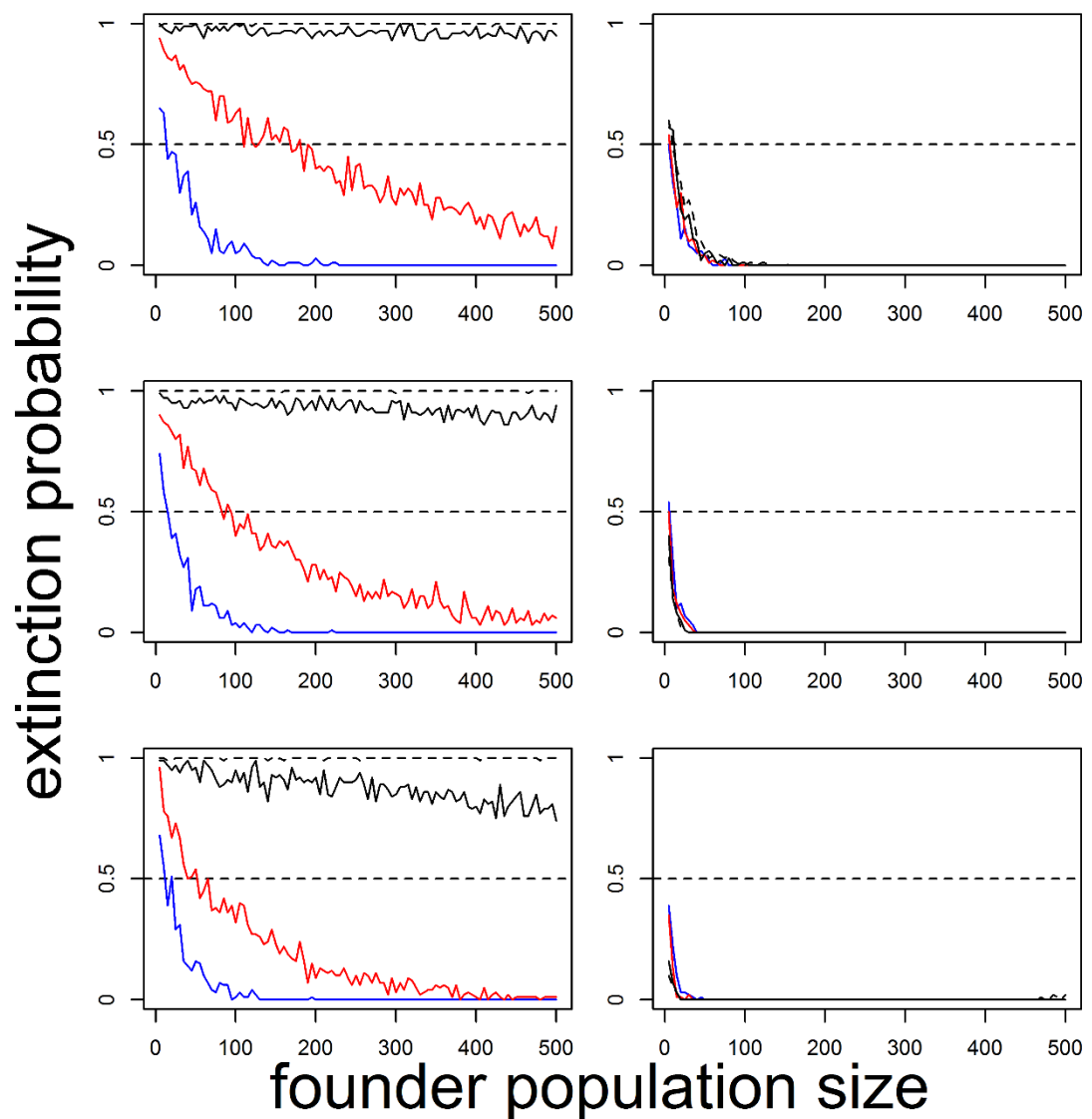
Figure 3 – The effect of founder population size on extinction probability in populations displaying either pre-copulatory (left) or post-copulatory (right) sexual cannibalism. The cannibalism rate was set to 20% (blue), 40% (red), 60% (black), or 80% (dashed). Sexual cannibalism could increase the average fecundity per mating by 20% (top row), 50% (middle row), or 80% (bottom row).

Mate encounter rate

Extinction probability had a negative sigmoidal relationship with mate encounter rate in both populations exhibiting pre-copulatory cannibalism and populations exhibiting post-copulatory cannibalism (Fig. 4). Thus, increasing first generation mate encounter rate reduced population extinction probability. For pre-copulatory populations, extinction

probability was lowest when cannibalism rate was set to 20%. Moreover, extinction probability was only less than 0.5 when pre-copulatory cannibalism rate was less than 80%, at 80% populations were always likely to go extinct, even when mate encounter rate and b were both high (Fig. 4, left). Increasing b had only a minor positive effect on the position of the sigmoidal curves in relation to mate encounter rate. For populations displaying post-copulatory cannibalism, the sigmoidal curves had a more obvious shift left as b increased, meaning that increasing b decreased the extinction probability overall. The lowest rates of post-copulatory cannibalism caused lower extinction probabilities when b was set to 20% (Fig. 4, top-right). However, as b increased, the effect of cannibalism on extinction probability was reversed such that when $b \geq 60\%$, higher rates of cannibalism led to lower extinction probabilities (Fig. 4, mid & bottom-right). In addition, post-copulatory cannibalism had an increasingly positive effect on per capita growth rate as b increased (Fig. 5). As such, when mate encounter rate was at its lowest and b was set to 100%, populations with the highest rates of post-copulatory cannibalism had the highest per capita growth rates (Fig. 5, bottom-right).
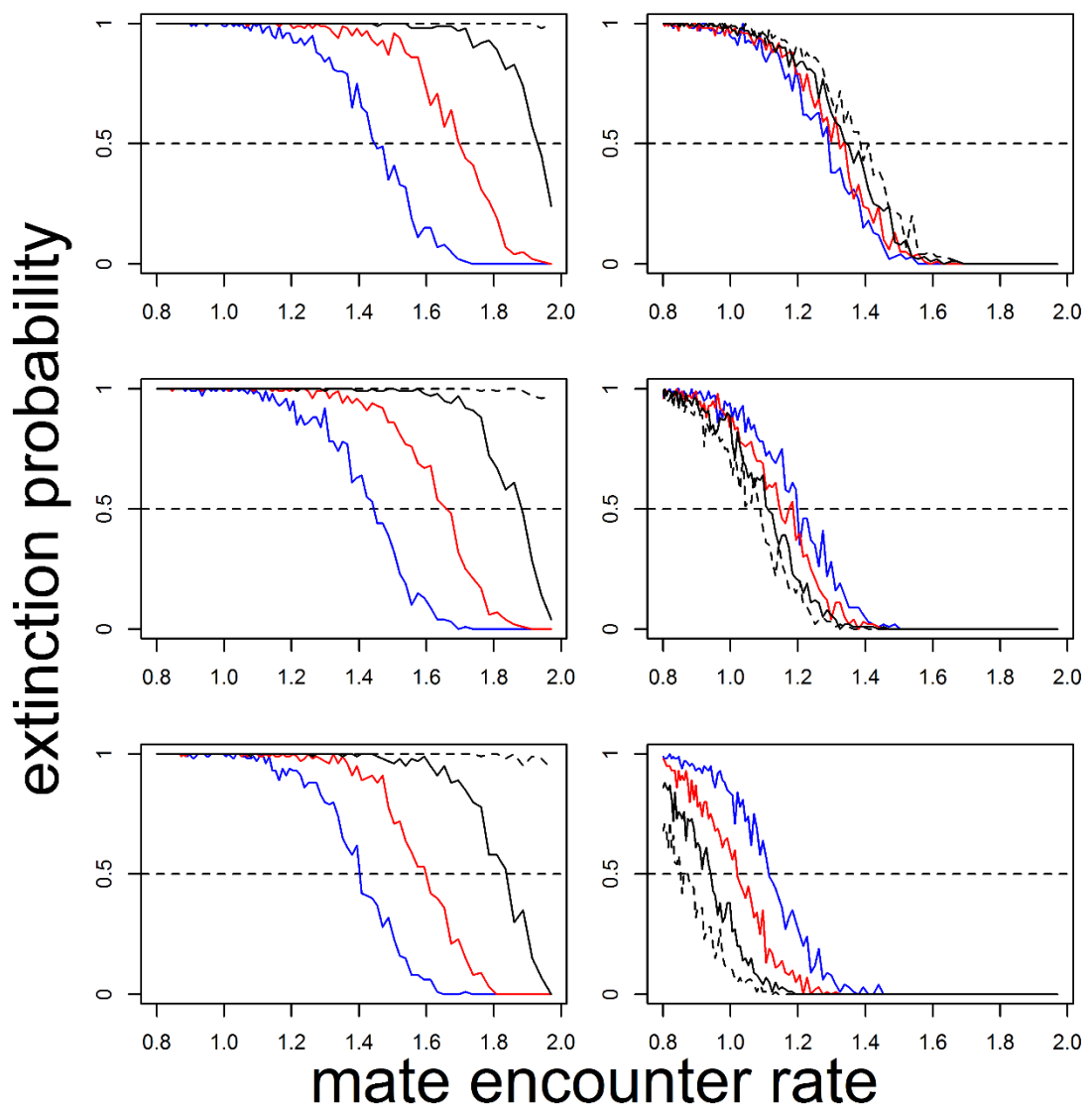
Figure 4 – The effects of first-generation mate encounter rate on population extinction probability in populations displaying either pre- (left) or post-copulatory (right) sexual cannibalism. Sexual cannibalism occurred at a rate of 20% (blue), 40%(red), 60% (black), and 80% (dashed). Sexual cannibalism can increase the average fecundity per mating by 20% (top row), 50% (middle row), or 80% (bottom row).
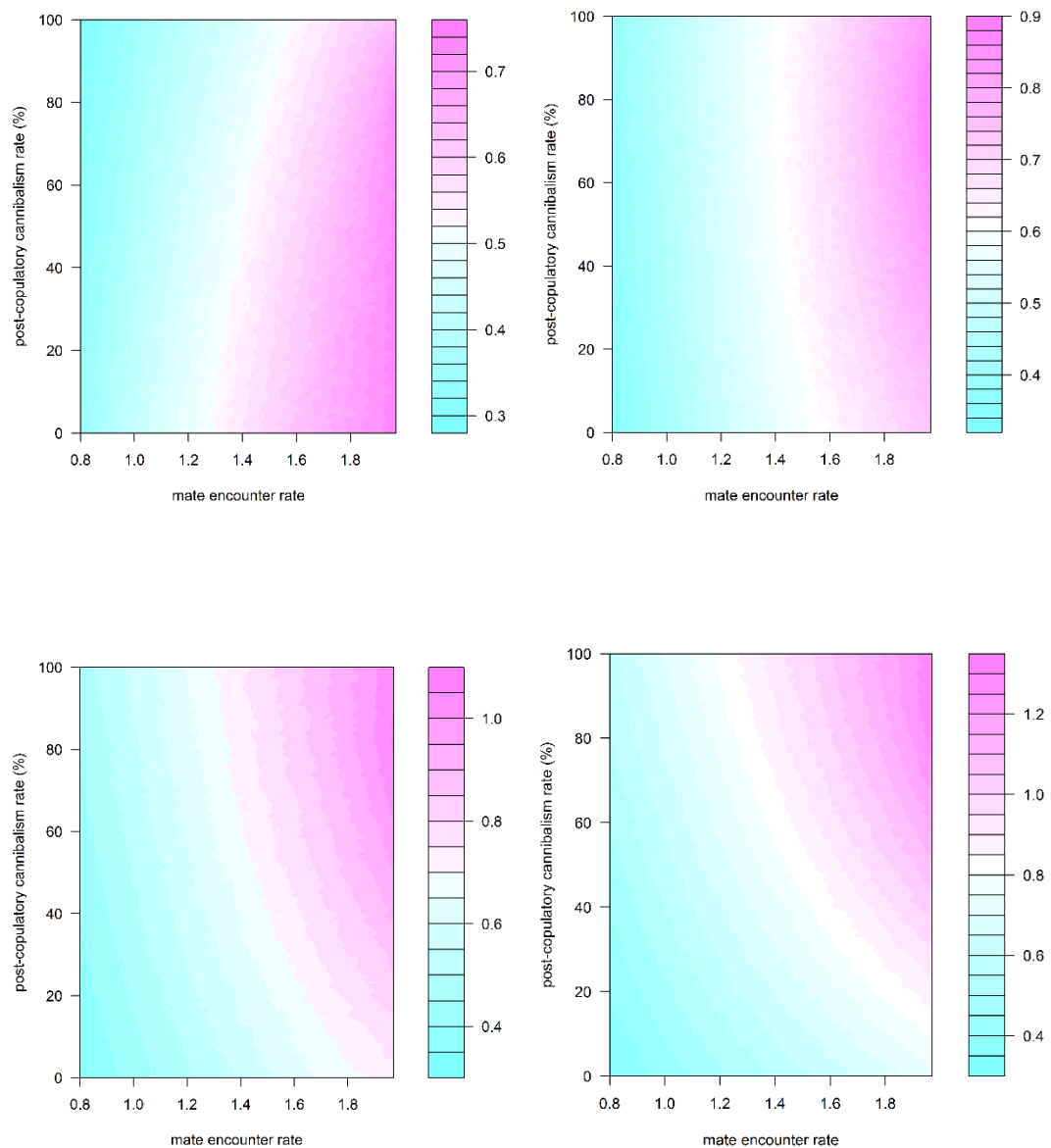
Figure 5 – The effect of first-generation mate encounter rate, post-copulatory cannibalism, and cannibalism-derived fecundity benefits per mating on per capita growth rate (r). Values on the colour bar correspond to r. The different panels refer to different amounts of cannibalism-derived increase in fecundity per mating: top left – 0%, top right – 30%, bottom left – 60%, and bottom right – 100%.

Discussion

Our models have shown that sexual cannibalism can affect the probability of population

extinction in response to the abundance and density of potential mates. The strength and

direction of these effects were dependent on the type of sexual cannibalism (pre- or post-

copulatory) and the fecundity increase that females could gain by cannibalising males. We found a strong effect of mate-encounter rate on extinction probability for populations displaying both pre-copulatory and post-copulatory cannibalism. This relationship took the form of a negative sigmoidal curve and created extinction thresholds where a small change in mate-encounter rate could lead to a large change in extinction probability (Fig. 4). The presence of such thresholds is important for conservation, as crossing a threshold can cause a stable population to undergo a rapid decline in response to environmental change (Frankham, 1995). There is evidence from several empirical studies suggesting that such thresholds are present in nature and can cause populations to decline dramatically when mate availability is reduced past a particular point (Veit & Lewis, 1996; Lennartsson, 2002). Thus, sexual cannibalism may make populations particularly vulnerable to extinction via Allee effects.

In most of our simulations, increasing the rate of sexual cannibalism shifted the extinction threshold such that extinction was likely under a wider range of mate encounter rates; this was always true when cannibalism was pre-copulatory. Surprisingly, this trend could be reversed in populations displaying post-copulatory cannibalism. If post-copulatory cannibalism increased female fecundity by ≥50%, increasing cannibalism became beneficial for reducing extinction risk relative to mate-encounter rate. Similarly, we found that high fecundity benefits of sexual cannibalism increased the positive effect that post-copulatory cannibalism had on per capita growth rate. As such, at very low mate encounter rates, populations with the highest rates of post-copulatory cannibalism had the highest per capita growth rate (Fig. 6). This is likely to be because the benefits received by a female through devouring a male after copulation outweigh the negative population-level effect of killing a reproductive male when reproductive encounters are rare. Moreover, the population-level effects of killing a male are likely to be reduced in sparse populations where males will be less likely to encounter more females. Increasing the fecundity benefit

that a female could gain from devouring a male also shifted the extinction threshold in a way that reduced the range of mate encounter rates that could lead to population extinction. However, this shift was more subtle for populations displaying pre-copulatory cannibalism. This is perhaps to be expected given that pre-copulatory cannibalism inevitably increases the incidence of females dying as virgins in a population, and thus reduces the probability of a female being able to utilise any potential fecundity benefit gained from devouring a male.

Our results show that sexually cannibalistic populations are generally more likely to go extinct when founder population size is small. Also, extinction probability was always higher in populations exhibiting pre-copulatory cannibalism as opposed to post-copulatory cannibalism (Fig. 3). For pre-copulatory cannibalism, larger founder population sizes did not substantially reduce extinction risk unless cannibalism rates were ≤40%. This may be due to the high levels of male mortality associated with higher cannibalism rates leading to low mating rates (Fig. 2), forcing extinction rates to remain high. At high pre-copulatory cannibalism rates, even when population size is large, the number of males that mate successfully is still likely to be low due to a large proportion of males dying just before copulation. As such, it may be that only populations in which females have a large abundance of males at their disposal can persist whilst displaying high rates of pre-copulatory cannibalism. Interestingly, there is evidence for male –biased sex ratios in many orb-weaving spiders known to display pre-copulatory cannibalism (Newman & Elgar, 1991; Zimmer, Welke & Schneider 2012), suggesting that it may be possible for a male-biased sex ratio to prevent population or local extinctions. For post-copulatory cannibalism, extinction risk was only >0 at very low population sizes and was not sensitive to changes in cannibalism rate. Although post-copulatory cannibalism results in the death of a male, it does not prevent the female from mating. Therefore, unless there are very few males in the population, such that each one represents a significant proportion of breeding males,

then the removal of males after copulation may not have much of an impact on mating rates.

It is well known that rapid human-induced habitat change causes some behaviours that were previously beneficial for an organism to become maladaptive (Sih, Ferrari & Harris, 2011; Robertson, Rehage & Sih 2013). Although there are numerous studies demonstrating the potential fitness benefits of pre-copulatory cannibalism to females (Prenter, MacNeil & Elwood 2006; Barry, Holwell & Herberstein 2008), these benefits are likely to be dependent on the environment. According to our results sexually cannibalistic populations are more likely to go extinct if: 1) populations are sparse or small, 2) cannibalism rates are high, or 3) the fecundity benefits associated with cannibalism are low. A decrease in density is a well-known side-effect of habitat degradation. However, increased rates of cannibalism and a reduction in the fitness benefits associated with cannibalism may also occur as a result of poor habitat quality. For example, individuals that develop in poorly resourced habitats may be smaller as adults. This could increase rates of sexual cannibalism in groups such as the wolf spiders (family: *Lycosidae*), where sexual cannibalism is used as a method of mate choice and small males are eaten by females more regularly (Persons & Uetz, 2005; Gibson & Uetz, 2008). Smaller males from poor quality habitats may also be a less valuable food source for females, thus reducing their capacity to boost female fecundity. Additionally, if poor quality habitat leads to a reduction in food resources, species in which sexual cannibalism is linked to female hunger may experience increased rates of cannibalism (Barry, Holwell & Herberstein 2008). In some species, the frequency of sexual cannibalism is known to be dependent on a male's ability to approach a female undetected. A study of the Chinese mantis *Tenodera sinensis* showed that males which were reared in low female-density environments were less cautious when approaching potential mates and were therefore more likely to be cannibalised (Brown et al. 2012). These results can be explained by cannibalism being less likely to deprive males of future reproductive encounters when

female abundance is low, thus the cost of cannibalism to males is reduced at lower population densities. Therefore, low density may also increase sexual cannibalism rates by causing changes in male behaviour. In summary, the negative population-level effects of sexual cannibalism may be exacerbated under poor environmental conditions through an inability to find a sufficient number of potential mates, increased rates of cannibalism, and decreased cannibalism-derived fitness benefits.

Despite the potential for sexually cannibalistic populations to experience strong Allee effects, it may be that some species can mitigate the negative effects of small population size and low-density by utilising adaptations not included in our model. Female springbok mantises *Miomantis caffra* significantly increase their risk of virgin deaths by cannibalising males prior to copulation at a rate of up to 62% (Fea et al., 2013; Walker & Holwell, 2016). However, female *M. caffra* can ensure reproduction using parthenogenesis to reproduce asexually (Walker & Holwell, 2016). Therefore, it could be that parthenogenesis has evolved in some sexually cannibalistic species to provide females with reproductive insurance in the case of low male abundance. Adult females of some sexually cannibalistic species, in particular praying mantids, are known to signal their presence to males using long range chemical cues (Holwell, Barry & Herberstein 2007; Lelito & Brown, 2008; Barry, Holwell & Herberstein 2010; Maxwell, Gallego & Barry 2010). Such long-range signalling could help to maintain mate encounter rates when population density is low by attracting males that are far away. In addition, adult male praying mantids are often capable of sustained flight (Ghose, Triblehorn, Bohn, Yager & Moss 2009), an attribute which is known to reduce the impact of low population density on mate-encounter rate in other species (Denno, 1994; Driscoll & Weir, 2005).

Our model assumes that initial adult sex ratios are equal, however this is not always the case in nature. In cannibalistic orb-weaving spiders, male biased sex ratios are common.

For example, in the large orb-weaving spider *Nephila plumipes*, several males can be found simultaneously on the web of a female (Elgar & Fahey, 1996). Having a surplus of males could reduce the risk of cannibalistic females "running out" of males in low density environments. However, increased male presence does not always equate to higher mating opportunities for females. In the highly cannibalistic orb-weaver *Argiope bruennichi*, females usually only mate once in their lifetime despite having a male biased sex ratio (Zimmer, Welke & Schneider 2012). Low mating rates in orb-weavers have been suggested to be in-part due to male choosiness and high male mate-search mortality rates (Kasumovic, Bruce, Herberstein & Andrade 2006). In summary, there are specific ecological and behavioural mechanisms that may help to prevent low mate abundance from reducing individual fitness and extinction risk in some species.

To our knowledge, there is no evidence to support the idea that sexual cannibalism rates are plastic in response to male availability. There is however, perhaps unfortunately for natural populations, evidence to suggest that rates of sexual cannibalism can be fixed across ecological contexts. In 1997, Arnqvist and Henriksson attempted to explain the high rates of pre-copulatory cannibalism seen in nursery-web spiders (family: *Pisauridae*) by suggesting that sexual cannibalism was a by-product of selection for high juvenile aggression towards prey. This theory was termed the "aggressive spillover hypothesis" and proposed that aggression could be fixed across contexts within individuals, potentially due to genetic constraints. Since then, studies on the six-spotted fishing spider (*Dolomedes triton*) have found evidence supporting the original hypothesis (Johnson & Sih, 2005; Johnson & Sih, 2007). According to our results, if pre-copulatory cannibalism rates are maintained in environments with low mate-encounter rates, populations could be threatened by a very high probability of extinction. The western Palearctic fen raft spider *Dolomedes plantarius* is part of a genus where pre-copulatory cannibalism is known to occur and has recently been classified as vulnerable (IUCN, 2012). Although the decline of

D. plantarius has largely been attributed to declines in habitat availability and quality (Smith, 2000; Leroy et al., 2013), we suggest that sexual cannibalism may also be a contributing to population decline by decreasing reproduction rates. The collection of more empirical behaviour and population data would be invaluable for making a reliable case for the role of sexual cannibalism on extinction risk in declining habitats.

Although sexual cannibalism is often regarded as a novel behaviour, it is fairly common among the praying mantids and spiders that have been studied. Both mantids and spiders are top invertebrate predators and are likely to have a large influence on ecosystem structure, particularly spiders, which are often regarded as a keystone group (Wise, 1995; Schmitz & Suttle, 2001). Our study has provided the first insights into the effect of sexual cannibalism on extinction probability in small or sparse populations. We have shown that extinction probability in sexually cannibalistic populations is highly sensitive to mate-encounter rate. The position of the extinction threshold is dependent on the rate of sexual cannibalism, whether cannibalism happens before or after copulation, and the extent to which cannibalism can increase fecundity. Very few studies have explored how the ecological impact of male-female reproductive encounters interacts with changes in the environment. We suggest that conservationists should pay close attention to species in which a high male-female encounter rate is necessary to ensure successful breeding.

CHAPTER 3: Density-dependent aggression, courtship and sex ratio in the fishing spider *Dolomedes fimbriatus*

Abstract

Sexual cannibalism is common in spiders and some species of insect. Sexual cannibalism can be advantageous for female fitness by preventing starvation and increasing egg production. However, it is possible that under low mate density, females may be at an increased risk of consuming all of the males they encounter prior to copulation, resulting in virgin death. Cannibalistic females may be able to mitigate the increased risk of virgin death if they reduce cannibalism rates in response to low mate availability. In this study we attempted to manipulate perceived mate density and observe whether it affected female aggression towards males. We observed how often female fen raft spiders (*Dolomedes fimbriatus*) attempted to attack courting males in response to successive mate encounters and predicted that an increased number of encounters would signal high mate density. Thus, female attack rate would increase as the number of males they encountered increased. We also recorded male courtship effort. Despite previous literature finding that *D. fimbriatus* females were highly aggressive towards conspecific males, we found that females only attacked courting males in 14% of encounters. None of these attacks resulted in cannibalism. Moreover, attacks were not associated with how many males the female had previously been exposed to. Male courtship effort decreased in response to repeated exposure to females. Interestingly, some of the virgin females laid and guarded unfertilised egg cases, this made them unattractive such that males would not court or approach them. Our results suggest that female *D. fimbriatus* are less aggressive towards males than previously thought, this may prevent sexual cannibalism from increasing their risk of virgin death in response to low mate availability. However, laying premature egg cases could shorten the timeframe in which females are attractive to males, potentially reducing their chance of encountering males, particularly in sparse populations.

Introduction

Behavioural plasticity, the ability of organisms to modify their behaviour to suit the environment, can play a crucial role in determining population viability (Hoare et al., 2007; Chevin et al., 2010). This is particularly true for populations in habitats that are rapidly declining in quality due to human impacts. As such, it is now more important than ever to understand how animals change their behaviour in response to different environmental scenarios (Sih et al., 2011). Behaviours are likely to vary in how influential they are in determining the fate of an individual or a population in a changing environment (Schlaepfer et al., 2002). One behaviour that may be particularly important in a changing habitat is mating behaviour, as it is fundamental for facilitating reproduction and the persistence of a population. However, there are many factors that may reduce mating success in changing habitats. For example, low population density is a known product of habitat disturbance (Andren, 1994) and can negatively affect both individual fitness and per capita growth rate via reduced mate encounter rates (Gascoigne et al., 2009). If an organism can alter its reproductive behaviour when potential mates are rare, it may help to mitigate the reduction in mate encounter rates. In several species there is evidence to suggest that individuals can modify behaviours to maintain mate encounters in sparse populations; for example, by relaxing mate rejection rate or increasing mate searching rate (Lehmann, 2007; Holwell et al., 2016). However, it is also possible that some species may be unable to mitigate reductions in mate density by modifying their behaviour, particularly if similar changes in density have not occurred in the species' recent evolutionary history (Rhainds, 2010; Sih et al., 2011).

One behaviour that might reduce mating rates in a changing habitat is sexual cannibalism (Fisher et al 2018). Sexual cannibalism typically involves a female devouring a male immediately before, during, or immediately after copulation. It has been formally observed in a variety of predatory invertebrates, but has been most commonly reported in spiders

(Birkhead et al., 1988; Elgar & Nash, 1988; Arnqvist, 1992; Kralj-Fišer et al., 2016). In all instances of sexual cannibalism, a reproductive male is removed from the population, potentially increasing male scarcity. Moreover, in the case of pre-copulatory cannibalism, as well as killing a male, females may directly increase their risk of virgin death. Theoretical studies have shown that sexual cannibalism, in particular pre-copulatory cannibalism, can have a negative impact on individual fitness and population viability under certain ecological conditions, in particular low mate density (Wilder et al., 2009; Fisher et al., 2018; Fisher et al., unpublished data). This negative impact of sexual cannibalism could be mitigated if cannibalism rates decline in changing habitats. There is some evidence of this kind of behavioural plasticity in some cannibalistic species where females reared in low density environments are less likely to cannibalise potential mates (Johnson, 2004; Rabaneda-Bueno et al., 2008). However, in the absence of behavioural plasticity, females may continue to cannibalise males at a high rate, meaning that the probability a female will consume all of the males she encounters will increase as mate encounter rate decreases. Thus virgin death rates may increase as a result of low density (Wilder et al., 2009; Fisher et al., 2019).

Female fishing spiders (family: Pisauridae) are known to be particularly aggressive towards potential mates and in some species are known to attempt to cannibalise nearly all approaching males (Arnqvist, 1992; Johnson & Sih, 2005; Schwartz et al., 2013; Schwartz et al., 2016). Furthermore, a lack of variation in cannibalism rates in response to different environmental contexts has also been demonstrated in some fishing spiders (Arnqvist, 1992; Johnson, 2001), thus it is possible that cannibalism may not be plastic in response to environmental cues for mate density.

Here we investigate cannibalism in the fen raft spider, *Dolomedes fimbriatus*. *D. fimbriatus* is found throughout Western Europe and is one of only two fishing spiders found in the

United Kingdom (Duffey, 1995), the other being the congeneric and critically endangered *Dolomedes plantarius* (Smith, 2000; Leroy et al., 2013). Penultimate instar and adult female *D. fimbriatus* are specialist hunters that rely on areas of freshwater to catch their prey. Due to their specific habitat criteria, populations of *D. fimbriatus* may be particularly vulnerable to decline if habitats are damaged. Indeed, specific habitat requirements may have exacerbated the negative effects of habitat change that led to the recent decline (Smith, 2000) and predicted continued decline of *D. plantarius* (Leroy et al., 2013). Discovering whether or not sexual cannibalism is plastic in response to mate density would help us to understand if cannibalism can accelerate population decline in damaged habitats, and may have implications for the conservation of *Dolomedes spp.* in the UK.

In this study we aimed to manipulate perceived mate density in adult female *D. fimbriatus* to test whether female aggression is affected by mate availability. We predicted that, to reduce the risk of virgin death, females would be less aggressive towards males when male density was perceived to be lower. We also predicted that older virgin females would be less likely to attack approaching males, again, to reduce their risk of virgin death. High male courtship effort has previously been shown to reduce cannibalism risk in spiders (Hebets & Uetz, 2000; Prenter et al., 2006); as such, we predicted that male courtship latency (a common proxy for courtship effort (Eastwood, 1977; Wilgers & Hebets, 2012)) would be positively associated with cannibalism. Finally, we predicted that male courtship effort would be energetically constrained and thus decrease in response to repeated exposure to females.

Methods

Recording, collection and rearing

I collected the spiders at Thursley Common Nature Reserve, situated in the Southwest of England, and comprised mainly of heathland bog. There is a wooden boardwalk that intersects the reserve which provided a consistent sampling transect and allowed for safe

access to the bog pools. I visited the reserve a total of 10 times over two years (2016 and 2017) between the months of April and June. On each visit I walked the entire length of the boardwalk and looked for *D. fimbriatus* in the adjacent pools. Upon locating a spider, the sex of the individual was recorded before an attempt at capture was made. Typically, it is only possible to confidently differentiate between males and females by casual observation after they have reached their penultimate instar. At this stage, males have a considerably smaller thorax and abdomen relative to their leg length, and the legs of the male appear significantly thinner than those of the female. A mixture of juvenile and adult males were collected; however, only juvenile females were taken to ensure that all females used in laboratory experiments were virgins. Individuals were then returned to the lab, kept at 22°C and housed in ventilated 75x210x130mm (HxWxD) plastic containers containing water to a depth of ≈ 1cm and a small piece of slate which formed a dry island that acted as a refuge. Enclosures were cleaned regularly and individuals were fed juvenile crickets (*Gryllus sp*.) *ad libitum*.

Behavioural trials

Behavioural trials took place in large 170x530x340mm (HxWxD) enclosures containing water to a depth of ≈ 2cm. All females used in the trials had been adults for at least 23 days and the mean female age (time since final moult) was 40 days. A small rock was placed at either end of the enclosure to form two islands. Because adult female *D. fimbriatus* have a tendency to become stressed upon being moved between enclosures (pers. obs. by A. Fisher), females were introduced to the trial enclosure the day before the trial took place and were left there overnight. This was intended to reduce the chance of any observed aggression towards the male being the result of stress due to human interference. Leaving females in the enclosure overnight also gave them the opportunity to explore the enclosure and lay down silken draglines. Silken draglines are known to induce courtship behaviour in males of several spider species including *D. fimbriatus* (Tietjehn, 1977;

Arnqvist, 1992). To begin the trial, males were introduced to the rock island at the opposite end of the enclosure to the female. I then recorded the length of time it took before the male began courting the female, and whether or not the female attacked the male. Male courtship and approach behaviour consisted of intermittent bouts of the male using his forelegs to tap the female dragline and the surface of the water, whilst traversing the dragline towards the female. Trials were terminated if the male took longer than 15 minutes to begin courting, stopped courting for over 15 minutes, or made contact with the female. If contact was made, trials were terminated so that males and females would remain as virgins for the subsequent trials. To manipulate the females' perception of male density, I introduced a new male to the female on each of the following two consecutive days, giving each female a total exposure to three males. Increased exposure to conspecifics in the lab has been shown to induce density-dependent behavioural responses in other species of predatory invertebrate (Rabaneda-Bueno et al., 2008; Brown et al., 2012). 17 males were used in trials with 11 females, and no females were paired with the same male twice. After the behavioural trials had been completed, the spiders continued to be cared for in the lab. During this time, five virgin females laid and guarded unfertilised egg cases. Further behavioural trials (using the same method) were performed on these females to test whether females continued to attract males after laying an unfertilised egg case.

Statistical analyses

Female aggression was analysed using a Generalised Linear Mixed-effects Model (GLMM) with a binomial error structure. Attack (binary) was the response variable, the fixed effects were: female age (time since final moult), the number of males the female had previously been exposed to, and male courtship latency. Because our experimental design involved repeated measures of the same females, female ID was included in the model as a random effect. Male courtship latency in response to repeated exposure to females was analysed

using a GLMM with a Gaussian error structure where the response variable was latency to

begin courting (seconds) and the fixed effect was trial number. Because repeated measures

of the same males were used, male ID was included in the model as a random effect. To

test whether an increase in age was associated with a change in courtship latency, I

conducted a Spearman's rank correlation test between age increase over trials and

courtship latency. Finally, to test how the abundance of males and females changed across

the season, a Generalised Linear Model (GLM) with a Poisson error structure was used. The

fixed effects were an interaction term between sex and time (number of days from the first

day of sampling) and an interaction term between sex and time^2. Time was included as a

quadratic term to test for the presence of a non-linear relationship between abundance

and time. Due to the fact that only five females laid unfertilised egg cases, no formal

analysis was carried out on the effect that laying an unfertilised egg case had on male

courtship behaviour.

Results

Out of a total of 29 trials, females were only observed attacking males in four of the trials.

In all cases, the female attacked the male prior to copulation. Males always managed to

escape the female, thus none of these attacks resulted in cannibalism. The likelihood that a

female would attack a male was not significantly associated with female age (df = 26, z =

0.194, p = 0.846), the number of males the female had been previously exposed to (df = 26,

z = -0.333, p = 0.739), or male courtship latency (df = 26, z = -0.990, p = 0.322). However,

courtship latency was significantly greater for males who had previously been exposed to a

female (Fig. 1: df = 30, z = 2.534, p = 0.0223). There was no significant correlation between

the amount of time between trial 1 and 2 and courtship latency (*Spearman's rank

correlation rho* = -0.378, S = 771.82, p = 0.165), implying that an increase in age was not

responsible for the increase in courtship latency. Spiders continued to be cared for in the

lab after the behavioural trials were completed. During this time, five virgin females laid

and guarded unfertilised egg cases. Upon being exposed to these females, males gave no indication of attempting to court. This suggests that, despite still being virgin, females that lay unfertilised egg cases cease to be attractive to males.
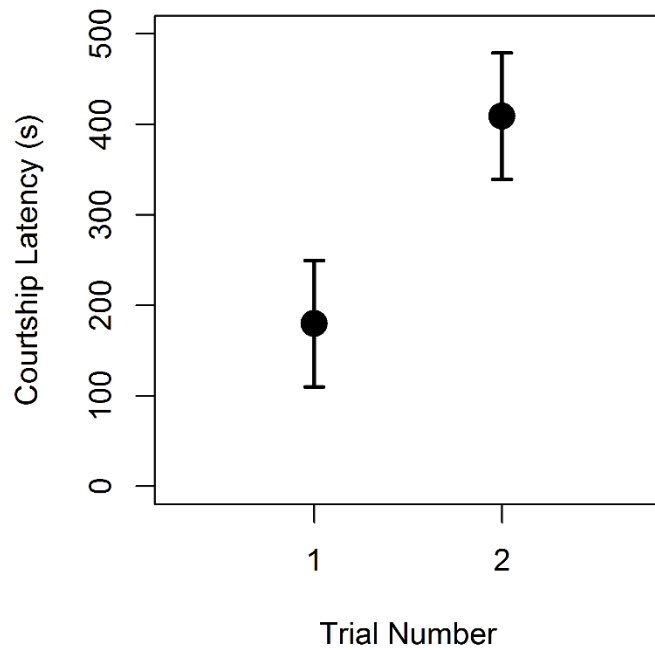
Figure 1 –Mean time taken for a male *Dolomedes fimbriatus* to begin courtship in their first and second exposure to virgin females. Error bars indicate 95% confidence intervals.

Over the 10 sampling visits, 75 males and 30 females were recorded. Although males were more abundant than females, this difference was marginally non-significant (df=19, z = 1.851, p = 0.0642). Both male and female abundance between the months of April and June had a significant negative relationship with time^2 (Fig. 2: Males: *df* = 19, *z* = -6.809, *p* < 0.0001; Females: *df* = 19, *z* = -2.272, *p* = 0.0231). There was a marginally non-significant interaction between abundance and sex over time (*df* = 19, *z* = 1.861, *p* = 0.0628).
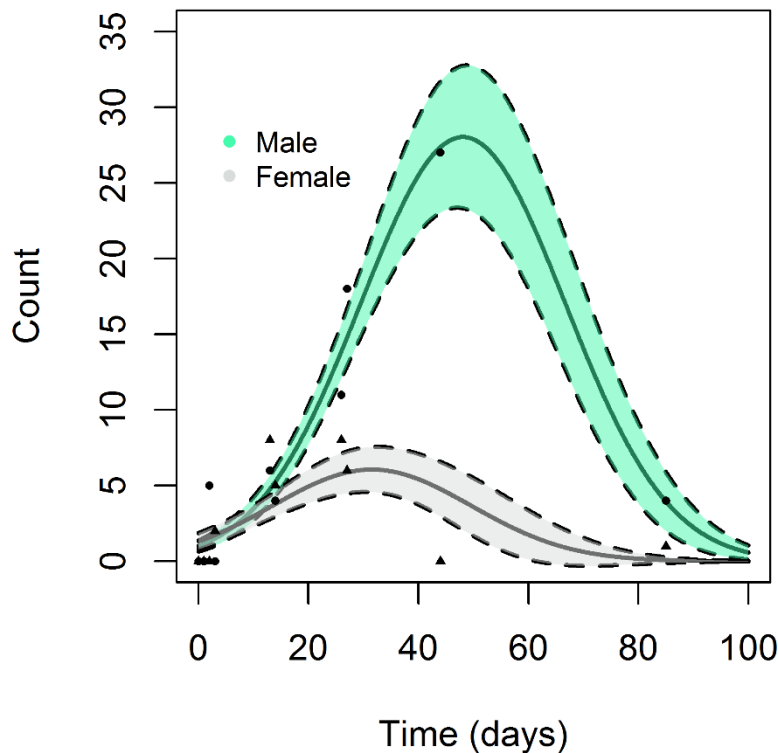
Figure 2 – Male (circular points) and female (triangular points) *Dolomedes fimbriatus* abundance in response to time after April 23rd. Data was collected from April - June in 2016 and 2017. Shaded areas indicate 95% confidence intervals.

Discussion

In this study, *D. fimbriatus* were far less aggressive towards males than has been shown in previous studies on *D. fimbriatus* and other species of the genus *Dolomedes*. Attack rates were very low and we found no effect of female age, perceived mate density or male courtship effort on the likelihood that a female would attack an approaching male. However, we have shown that courtship latency in males increased significantly upon being exposed to a second female, implying that there has not been strong selection for males that have consistent courtship behaviour. We have also shown that females that lay an unfertilised egg case become unattractive to reproductive males, despite the fact that they are still virgins, potentially lowering reproductive rates. Finally, we provide evidence that

the sex ratio is male biased, which is common in other spider species and will likely have important implications for mate availability and competition.

In the past, adult female spiders of the genus *Dolomedes* have been shown to be highly aggressive towards reproductive males. In 1992, Arnqvist reported that female *D. fimbriatus* attacked courting males in 87% of encounters. Similarly, female *D. tenobrosus* have been shown to attack males prior to copulation in up to 68% of encounters (Schwartz et al., 2014). In this study, we found that females only attacked males in only 14% of encounters. One possibility for these comparatively low attack rates could be due to female satiation removing the requirement for females to consume males in order to obtain nutrients (Barry et al., 2008). However, this goes against evidence in *D. triton* which suggests that female attack rate is not dependent on female body condition (Johnson & Sih, 2005). It could also be that the adaptive benefits of sexual cannibalism vary across different populations of *Dolomedes*, thus selecting for variation in aggression across populations. For example, in habitats where individuals are sparse and mate encounter rates are low, females may be selected to maximise their chance of being fertilised by lowering their pre-copulatory attack rates. Behavioural divergence across populations may be particularly common in *D. fimbriatus* which, due to their specific habitat requirements and lack of long range dispersal ability, may be likely to form geographically isolated populations (Suter, 1999; Vugdelić, 2006; Duffey, 2012; Leroy et al., 2013). As such, genetic mixing with neighbouring populations is highly unlikely to occur, allowing behaviours to evolve to suit particular challenges imposed by specific habitats.

It is fairly common for female spiders and insects to cease to attract males once they have mated, particularly if approaching a female is potentially costly due to cannibalism risk (Lelito & Brown, 2006; Gaskett, 2007). Attractiveness to males is often thought to be associated with pheromone production, so a reduction in the attractiveness of mated

females is likely to be due to reduced pheromone production (Roberts & Uetz, 2005). Here we report an unusual circumstance in which virgin females cease being attractive to males following the oviposition of an unfertilised egg case. To our knowledge, this has not been shown previously in *Dolomedes* and may not have been found in other spiders. Becoming unattractive to males before being mated is likely to increase a female's probability of dying a virgin, particularly in sparse populations where mate encounter rate is low. As such, one would expect strong selection against this. It may be that encounters with males in the wild are common, and thus the risk of a female remaining unmated is low, meaning that there is little to no advantage of remaining attractive to males for a long period of time. Male-biased operational sex ratios (OSR) are commonly reported in orb-weaving spiders (Fromhage et al., 2007; Fromhage et al., 2008) and have also been seen in *Dolomedes triton* (Zimmermann & Spence, 1992). Conditions such as a male-biased OSR, which has been suggested by this study (Fig. 2), may lead to an excess of males being available to females. This would increase the probability that females will mate early in their adult life, and remove the need for females to remain attractive to males for an extended period of time. In addition, there is evidence to suggest that pheromones produced to attract males can bear a significant energetic cost in some species of spider (Baruffaldi & Andrade, 2015). Therefore, it may be advantageous for females to stop producing pheromones if they are likely to have mated, as this will allow them to allocate more energetic resources into egg production.

Monogyny is fairly common in spiders, and evidence of male adaptation to monogyny in spiders is perhaps most obvious in instances where males sacrifice themselves after their first copulation to boost the fecundity of the female and delay her re-mating (Andrade, 2003; Schwartz et al., 2013). The occurrence of male-enforced monogyny is often hypothesised to have evolved in response to a low probability that males will get a second opportunity to mate, either because males are likely to be cannibalised by the first female

they encounter or because there is a high mortality risk associated with searching for females (Buskirk et al., 1984; Kasumovic et al., 2006). It would therefore be most adaptive for males to invest maximally in their first mating. In some spiders, increasing courtship effort is known to decrease the likelihood of cannibalism prior to copulation. In this study we show a reduction in male courtship effort in response to exposure to a second female. As such, males have not been strongly selected to display consistent mating behaviour, which is indicative of a system where males are unlikely to remate. However, because female attacks on males were uncommon, our evidence suggests that cannibalism is unlikely to be responsible for a lack of courtship consistency. Theoretical and empirical studies on spider mating systems indicate that male-biased sex ratios may be associated with the evolution of monogyny (Fromhage et al., 2005; Fromhage et al., 2008; Schneider & Fromhage, 2010). Therefore, we suggest that the high male-biased sex ratio demonstrated in this study may create conditions in which male competition is so high that the probability of a male getting access to a second virgin female is very small. Thus we provide evidence for the theory that male-biased sex ratios may be in part responsible for the evolution of males that are adapted for maximising their reproductive output during a single encounter with a female. It is also worth noting that males are often the dispersing sex in adult spiders (Andrade, 2003; Kasumovic et al., 2006). Therefore, male *Dolomedes fimbriatus* may be likely to be travelling between patches of water in search of females. Because we only surveyed spiders found on or immediately near patches of water, our counts may in fact underestimate the abundance of males in the habitat.

In this study, we have shown that female aggression towards potential mates can be rare in *Dolomedes* fishing spiders. This goes against the evidence provided by previous studies which show very high attack rates. We therefore think that aggression in *D. fimbriatus* may be population-specific and that differences across populations could have evolved to mitigate environmental challenges such as reduced mate availability. We also show that

virgin female *D. fimbriatus* become unattractive after ovipositing an unfertilised egg case. Although this may not reduce female fitness if females are likely to mate early in their adult lives, in sparse populations where males are rare, it could be that females increase their risk of dying as virgins by laying unfertilised egg cases. Our field data suggests that the OSR may be heavily male-biased. This may create high levels of competition among males for access to females, thus reducing the likelihood that males will be able to mate twice. This may explain why we found a significant reduction in male courtship effort in response to males being exposed to a second female. The mating dynamics of *Dolomedes fimbriatus* are still poorly understood but could play a vital role in determining species vulnerability to extinction. We suggest that a cross-population study observing how aggression towards males and female mating rate interacts with natural mate density would be valuable for designing conservation strategies for *Dolomedes*.

CHAPTER 4: The impact of behavioural syndromes on aggression in praying mantids

Abstract

Behavioural syndromes occur when behaviours are correlated within individuals. As such, the magnitude of certain behaviours may be partly predicted by other behaviours, rather than the environment. This can constrain behaviours, potentially reducing behavioural variability. Pre-copulatory sexual cannibalism, the consumption of potential mates before copulation, is an example of a behaviour that can be costly, as it can lead to cannibalistic females remaining unmated, particularly if males become rare. One possible explanation for the persistence of pre-copulatory cannibalism is that it is part of a behavioural syndrome, and is correlated with high levels of aggression towards prey. Here we test this in two species of praying mantis: the highly cannibalistic *Miomantis caffra* and the less cannibalistic *Orthodera novaezealandiae*. If cannibalism in *M. caffra* is due to a behavioural syndrome, we predicted that: 1) *M. caffra* would be more aggressive towards prey than *O. novaezealandiae*, 2) aggression towards prey would be correlated across juvenile and adult instars for *M. caffra* but not *O. novaezealandiae*, and 3) aggression towards prey would be associated with a propensity for sexual cannibalism among individual *M. caffra*. We found evidence supporting prediction one, but not predictions two and three. Surprisingly, aggression was shown to be repeatable and correlated across instars for *O. novaezealandiae* but not *M. caffra*. Our results suggest that behavioural syndromes do not pre-dispose individuals to sexual cannibalism, even in clades where sexual cannibalism is common. This suggests that sexual cannibalism evolves due to the direct benefits it brings to females, rather than being a by-product of high aggression.

Introduction

Behavioural syndromes occur when the behaviour of an individual remains consistent across contexts and/or correlates with one or more different behaviours (Sih et al. 2004). In

addition, behavioural syndromes have the potential to restrict behavioural variation within individuals (Pruitt et al. 2008), which may have implications for species' ecology (Pruitt and Riechart, 2012). For example, if a behavioural syndrome reduces behavioural plasticity (Sih et al. 2012), this may reduce how effectively individuals can modify behaviour in the face of environmental perturbations. One of the most commonly studied behavioural syndromes is aggression and its covariants. Individual variation in aggression is known to be consistent across developmental and environmental contexts in certain species (Arnqvist and Henriksson, 1997; Dingemanse et al., 2007) and can correlate with a variety of other behaviours that determine fitness (Smith and Blumstein, 2008). For example, some evidence suggests that aggressive individuals are better dispersers (Dingemanse et al. 2003; Cote et al. 2010), bolder in the presence of predators (Huntingford, 1976; Johnson and Sih, 2005) and more territorial (Riechart and Hedrick, 1993). Studies across several spider families have also shown that aggression towards prey is positively correlated with a propensity for pre-copulatory cannibalism; the killing and eating of potential mates prior to copulation (Arnqvist, 1992; Riechert and Hedrick, 1993; Arnqvist and Henriksson, 1997; Johnson and Sih, 2005; Pruitt et al. 2008; Rabaneda-Bueno et al. 2014).

Pre-copulatory cannibalism has been observed in several species of predatory invertebrates (Elgar, 1992) but is most commonly reported in praying mantids (Barry et al. 2009; Walker and Holwell, 2015) and spiders (Elgar and Nash, 1988; Wilder and Rypstra, 2008). Pre-copulatory cannibalism has the potential to be maladaptive for both sexes because males are killed and females increase their risk of dying as a virgin. As well as the individual-level costs, pre-copulatory cannibalism has the potential to reduce population growth rate and increase population extinction risk (Fisher et al. 2018). Currently, there are three main hypotheses for why pre-copulatory sexual cannibalism persists in nature: **1) adaptive foraging** – females devour males they encounter in order to gain essential nutrients for egg production (Hurd et al. 1994; Barry et al. 2008; Roggenbuck et al. 2011);

2) mate choice – sexual cannibalism represents an extreme form of mate choice in which non-preferred males are devoured to prevent copulation (Hebets 2003; Persons and Uetz, 2005; for a review see: Prenter et al. 2006); **3) aggressive spillover** – adult female aggression towards conspecific males is a by-product of strong selection for juvenile aggression (Arnqvist, 1992; Arnqvist and Henriksson, 1997; Johnson and Sih, 2005). As such, the aggressive spillover hypothesis (ASH) suggests that even though pre-copulatory sexual cannibalism may be costly for females, this cost can be offset by the benefits of high juvenile feeding rates.

If juvenile and adult aggression were decoupled, this would appear to benefit females, as they could display high hunting aggression as juveniles, without killing potential mates before copulation as an adult. Thus, one would expect strong selection for individuals that can dissociate aggression between hunting and mating contexts. However, there is evidence for a lack of lability in aggression in several species. In the fishing spider *Dolomedes triton*, female aggression towards prey is positively correlated with aggression towards conspecific males (Arnqvist and Henriksson, 1997; Johnson, 2001). Positive correlations between female aggression towards prey and the probability of attacking a potential mate have also been demonstrated in funnel-web spiders (Riechert and Hedrick, 1993), cob-web spiders (Pruitt et al. 2008) and a wolf spider (Rabaneda-Bueno et al. 2014). There is also evidence for positive correlations between juvenile and adult aggression towards prey in sexually cannibalistic species, this further supports the notion that aggression in sexually cannibalistic species is linked across contexts (Johnson and Sih, 2005).

However, if behavioural syndromes are a major factor in maintaining sexual cannibalism in nature, then there are two relatively untested predictions. Firstly, within clades that contain sexually cannibalistic species, species in which sexual cannibalism is absent or rare

may show lower levels of aggression towards prey than highly cannibalistic species. In other words, if sexual cannibalism is caused by selection for high juvenile aggression in females, then where there is strong selection against sexual cannibalism, this may constrain juveniles to displaying lower than optimal levels of aggression. Secondly, the evolution of contextually optimal levels of aggression in males of cannibalistic species may also be constrained. For example, males of cannibalistic species are also known to benefit from high juvenile feeding rates (Barry, 2013) and would benefit from being highly aggressive towards prey. However, if aggression in males of cannibalistic species is fixed across contexts, or aggression is correlated with other potentially maladaptive behaviours, then the evolution of male juvenile aggression may be constrained by the costs of males continuing to be aggressive into adulthood. For example, aggressive adult males may be bolder in the presence of females and thereby increase their risk of being cannibalised (Lelito and Brown, 2006).

Determining whether or not sexual cannibalism is part of a behavioural syndrome is important for understanding why the behaviour has evolved and is maintained in nature. Also, because behavioural syndromes can reduce behavioural plasticity (Sih et al., 2012), the presence of a syndrome in a cannibalistic species could have ecological implications (Fisher et al., 2018). We examined aggression across life-stages and context in two species of praying mantis residing in New Zealand: the highly sexually cannibalistic *Miomantis caffra*, and the less cannibalistic *Orthodera novaezealandiae*. We tested the following predictions: 1) female *M. caffra* will on average be more aggressive towards prey than female *O. novaezealandiae* as juveniles and adults, 2) female *M. caffra* will on average be more aggressive towards prey than male *M. caffra* as juveniles and adults, 3) juvenile aggression will correlate with adult aggression in *M. caffra*, and 4) adult aggression in female *M. caffra* will be positively correlated with the likelihood of attacking potential mates.

Methods

Study species

Two species of praying mantis were used in this study, *Orthodera novaezealandiae* and *Miomantis caffra*. *O. novaezealandiae* is the only praying mantis species known to be native to New Zealand, is most commonly found in open habitat and shrubland (Ramsay, 1990) and rarely cannibalises (Fea et al. 2013). *O. novaezealandiae* were collected from grassland and woodland areas around Auckland, NZ. The second species, *M. caffra*, is an invasive South African mantis that is estimated to have been introduced to New Zealand's north island in 1978 and is highly sexually cannibalistic. Moreover, sexual cannibalism in *M. caffra* is always pre-copulatory (Fea et al. 2013; Walker and Holwell 2015). *M. caffra* is now well-established in many areas of New Zealand's north island and is commonly found in suburban gardens. We collected *M. caffra* from the suburbs surrounding Auckland. Both species were collected from February - March 2017 and February 2019. To ensure that all individuals were virgin, only juveniles were collected. All mantids were housed individually in inverted 750ml plastic cups with a mesh ceiling, misted daily and fed houseflies (*Musca domestica*) *ad libitum*.

Aggression towards prey

Mantids were starved for two days prior to testing to standardise hunger levels and were weighed immediately before testing. Note that because insects are not known to vary significantly in size within instars (Chown and Gaston, 2010), weight can be compared within instars irrespective of age. The mantids were then placed in a six-sided plastic container measuring 70x120x80mm (HxWxD). When measuring predatory responses, using a virtual prey item can be useful for standardising the variation in activity that would be present in live prey (Ioannou et al. 2012). We created a moving virtual prey item (see digital supplementary material) in Adobe Macromedia Flash 8. The virtual prey item was displayed on a digital screen affixed to the side of the mantis' enclosure. Similar methods

have been used previously to induce predatory responses in praying mantids and jumping spiders (Yamawaki, 2003; Bartos and Minias, 2016). To quantify aggression, we recorded whether or not the mantis attacked the virtual prey. The mantis was given a maximum time of five minutes to attack the virtual prey. The mantis was then offered a single housefly and given a maximum time of 10 minutes to capture the fly. If the mantis consumed the fly, we would once again test the mantis' aggression towards the virtual prey. This process was repeated until: 1) the mantis stopped eating the offered flies, or 2) the maximum number of repeats (five) was reached. Repeating the process allowed us to compare aggression in response to changes in prior food consumption. This method was used for both *Miomants caffra* (n_{male} = 16, n_{female} = 16) and *Orthodera novaezealandiae* (n_{male} = 16, n_{female} = 14) at both the sub-adult (penultimate instar) and adult stages, such that a maximum of 10 repeats were conducted for each individual.

Aggression towards potential mates

To determine the likelihood that a female would cannibalise a male, a randomly chosen conspecific adult male was introduced to the opposite side of a large mesh enclosure containing an adult female. Mating trials (n = 12 for *M. caffra* and n = 7 for *O. novaezealandiae*) took place at night as there is evidence to suggest that male mantids are more likely to approach females after dusk (Fea et al. 2013; Walker and Holwell 2015). Males and females were paired between 19:00 and 20:00 and left for 12 hours. After 12 hours, we recorded whether or not the male had been devoured. We assumed that the consumption of males only took place in a mating context as female mantids are typically sit-and-wait predators (Hurd, 1999; Barry, 2013) and adult males are only known to approach females for the purposes of mating (Gemeno and Claramunt, 2006; Lelito and Brown, 2006). Individuals were used only once in mating trials.

Analyses

We used a generalized linear mixed-effects model with binomial error correction to determine whether the probability that an individual would attack the virtual prey item was affected by age, sex or species. The model consisted of a three-way interaction between age, sex and species,

$$attack \sim age * sex * species + (1|individual).$$

To determine whether certain groups became less aggressive due to satiating sooner, we constructed a second model which included the number of flies an individual had eaten immediately prior to exposure to the virtual prey item as a fixed effect,

$$attack \sim age * sex * species * flies + (1|individual).$$

We used a separate binomial GLM to test for a relationship between aggression towards prey and the probability that a female would cannibalise a male. To determine the effect of age, sex and species on individual weight we used the following generalised linear mixed-effects model with Gaussian error,

$$weight \sim age * sex * species + (1|individual)$$

We also used Spearman's rank correlation to see if there was a relationship between juvenile weight and juvenile attack frequency. Note that we did not attempt to correlate aggression with adult weight, as adult weight was more likely to have been a product of the standardised laboratory feeding regime as opposed to natural feeding rates. Spearman's rank correlations were also used to check for a relationship between juvenile attack probability and adult attack probability. Behavioural repeatability describes the consistency of individual traits relative to the variation of that trait in the sample population. We calculated repeatability for males and females in both species using the rptR package in R (Schielzeth & Nakagawa, 2011), where attack on the virtual prey item (binomial) was the response variable, repeat and age were fixed effects and individual/organism ID was a

random effect. The model was run for 1000 bootstrap repeats. All statistics were carried out in R version 3.3.0 (2016) and GLMMs were conducted using the lme4 package (Bates et al. 2015).

Results

Miomantis caffra aggression

There was a significant interaction between sex and life stage on overall attack frequency on the virtual prey for *M. caffra* (Fig. 1a; df = 56, z = 3.874, p < 0.001), meaning that the effect of age on aggression was different for male and female *M. caffra*. Sub-adult females had a higher attack frequency than sub-adult males, but this difference was non-significant (df = 56, z = 1.338, p = 0.181). However, adult attack frequency was significantly higher in females than in males (df = 56, z = 4.872, p < 0.001). Female attack frequency did not change significantly between the sub-adult and adult stage (df = 56, z = 0.556, p = 0.578), but adult males were significantly less likely to attack than sub-adult males (df = 56, z = -4.633, p < 0.001). Over the 12 cannibalism trials with *M. caffra*, five males were cannibalised. The frequency at which an adult female attacked the virtual prey was not significantly associated with whether or not the female would cannibalise a male (df = 11, z = 1.518, p = 0.129).

In sub-adult males and females, the probability of an individual attacking the virtual prey item was not significantly affected by the number of flies that had been consumed (Fig. 2a; males: df = 26, z = 0.171, p = 0.864; females: df = 26, z = 1.091, p = 0.275). Nor was there a significant interaction between the number of flies consumed and sex (df = 26 z = 0.682, p = 0.495). In adults, the effect of the number of flies consumed on attack probability was significantly different for adult males and females (Fig. 2b; df = 26, z = 2.704, p = 0.00685). Attack probability declined significantly in adult males in response to the number of flies they had been eaten prior to being exposed to the virtual prey, whereas attack probability

in adult females showed a marginally non-significant positive response to fly consumption (Fig. 2b; males: *df* = 26, *z* = -2.018, *p* = 0.0436; females: *df* = 26, *z* = 1.833, *p* = 0.0668).

Orthodera novaezealandiae aggression

There was a significant interaction between sex and life stage on attack frequency towards the virtual prey item in *O. novaezealandiae* (Fig. 1b; *df* = 56, *z* = 2.222, *p* = 0.026), meaning that the effect of age on aggression was different for males and females. Attack frequency was not significantly different between sub-adult males and females (Fig. 1b; *df* = 56, *z* = 0.031, *p* = 0.975). Adult female *O. novaezealandiae* had a marginally non-significant higher attack frequency than adult males (*df* = 56, *z* = 1.795, *p* = 0.072). Female attack frequency did not change significantly between the sub-adult and adult stage (*df* = 56, *z* = 0.951, *p* = 0.342). There was a marginal but non-significant trend for attack frequency to be higher in sub-adult than adult males (*df* = 56 *z* = -1.732, *p* = 0.083). Cannibalism was only observed once out of seven mating trials in *O. novaezealandiae*.

In sub-adult males and females, the probability that an individual would attack the virtual prey item was not significantly affected by the number of flies consumed (males: *df* = 23, *z* = -1.496, *p* = 0.135; females: *df* = 23, *z* = - 0.223, *p* = 0.823) and the interaction between sex and the number of flies consumed was also non-significant (*df* = 23, *z* = 0.817, *p* = 0.414). Similarly, the probability of individuals attacking the virtual prey item was not significantly affected by the number of flies consumed in adult females (*df* = 23, *z* = -0.617, *p* = 0.537), but the probability of adult males attacking the virtual prey item decreased significantly as the number of flies consumed increased (*df* = 23, *z* = -2.041, *p* = 0.0413). There was no significant interaction between the number of flies consumed and sex in adults (*df* = 23, *z* = 1.086, *p* = 0.277).
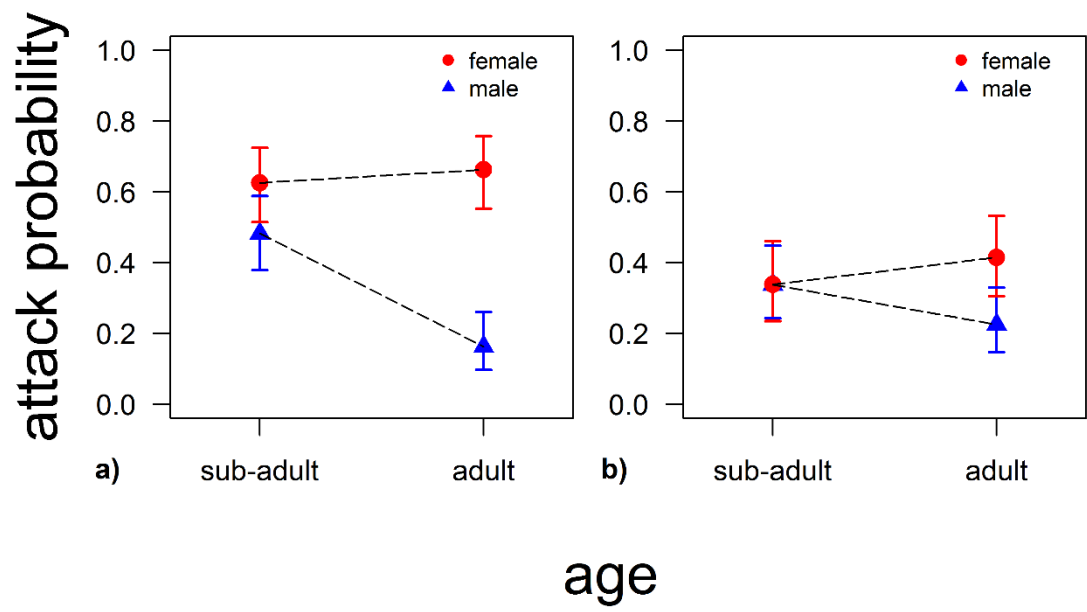
Figure 1 – Mean probability of attacking a virtual prey item in a) *Miomantis caffra*, and b) *Orthodera novaezealandiae*. Error bars indicate 95% confidence intervals.
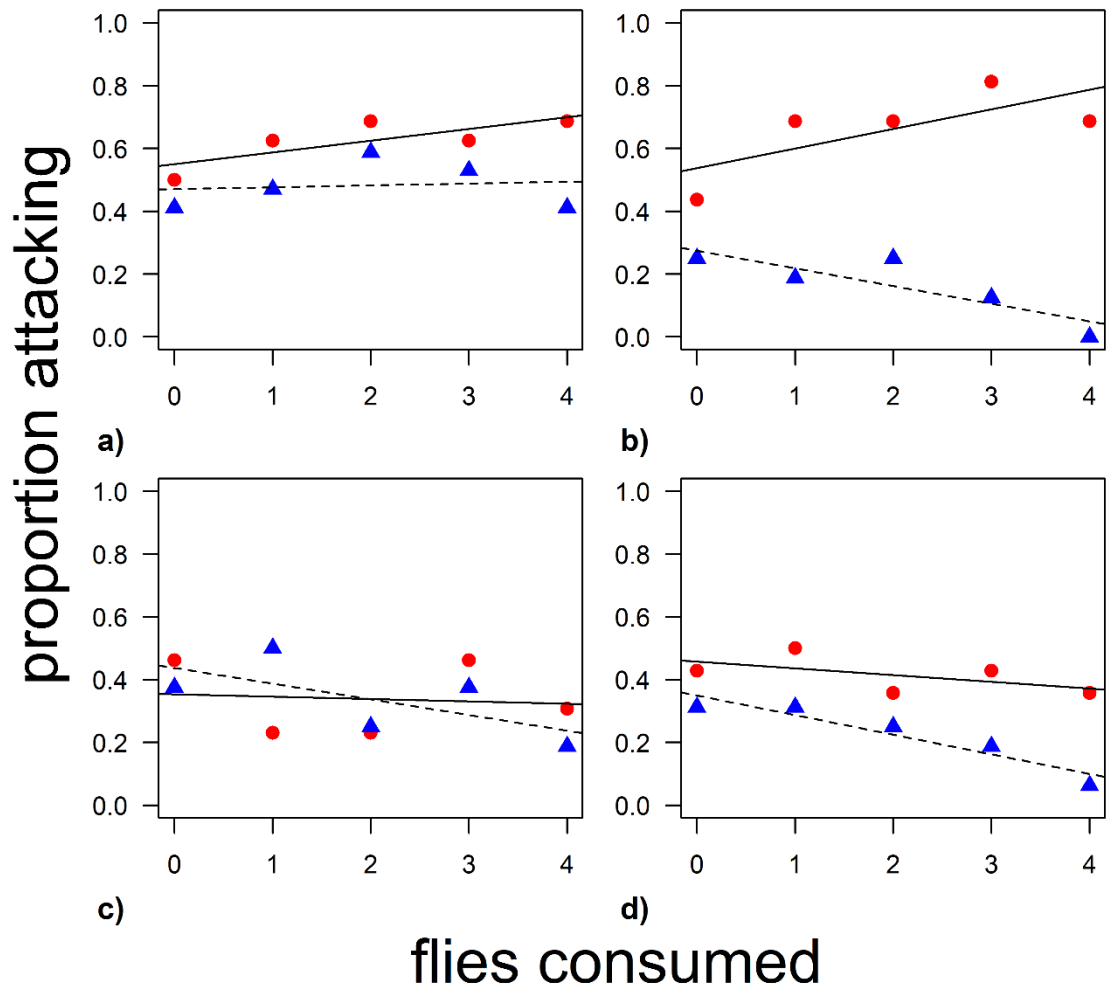
Figure 2 – Variation in attack rate on a virtual prey item in response to food intake (males = blue triangles, females = red circles) in, a) juvenile *Miomantis caffra*, b) adult *Miomantis caffra*, c) juvenile *Orthodera novaezealandiae*, and d) adult *Orthodera novaezealandiae*.

Comparison of aggression of both species

Attack rate in female *M. caffra* was significantly higher than that of *O. novaezealandiae* females at both the sub-adult and adult life stage (sub-adult: df = 56, z = 2.58, p = 0.01; adult: df = 56, z = 2.301, p = 0.021). Attack rates in male *M. caffra* did not differ significantly from that of *O. novaezealandiae* males in sub-adults or adults (sub-adult: df = 56, z = 1.452, p = 0.146; adult: df = 56, z = -0.882, p = 0.377). The three-way interaction between species, life stage and aggression was not significant (df = 56, z = 1.395, p = 0.163),

meaning that the difference in the effect of age on aggression in males and females was not different between *M. caffra* and *O. novaezealandiae*.

Repeatability

For male and female *M. caffra* we found no significant correlation between juvenile and adult attack rates (Fig. 3a; Spearman's rank: males: $S = 543.56$, *rho* $= 0.20$, $p = 0.46$; females: $S = 811.67$, *rho* $= -0.19$, $p = 0.47$). In *O. novaezealandiae* juvenile and adult attack rates were correlated in females but not males (Fig. 3b; Spearman's rank: males: $S = 519.95$, *rho* $= 0.235$, $p = 0.38$; females: $S = 86.795$, *rho* $= 0.762$, $p = 0.0025$). In concordance with the findings of Bell et al., (2009) for invertebrates, female aggression was more repeatable than male aggression for both *M. caffra* and *O. novaezealandiae* (Table 1). However, only aggression in female *O. novaezealandiae* was more repeatable than the average repeatability (0.32) calculated from a range of studies on other organisms (Bell et al., 2009). Thus, we found evidence for consistency in overall aggression and a behavioural syndrome between juvenile and adult aggression in female *O. novaezealandiae*, but not male *O. novaezealandiae* or either sex in *M. caffra*.
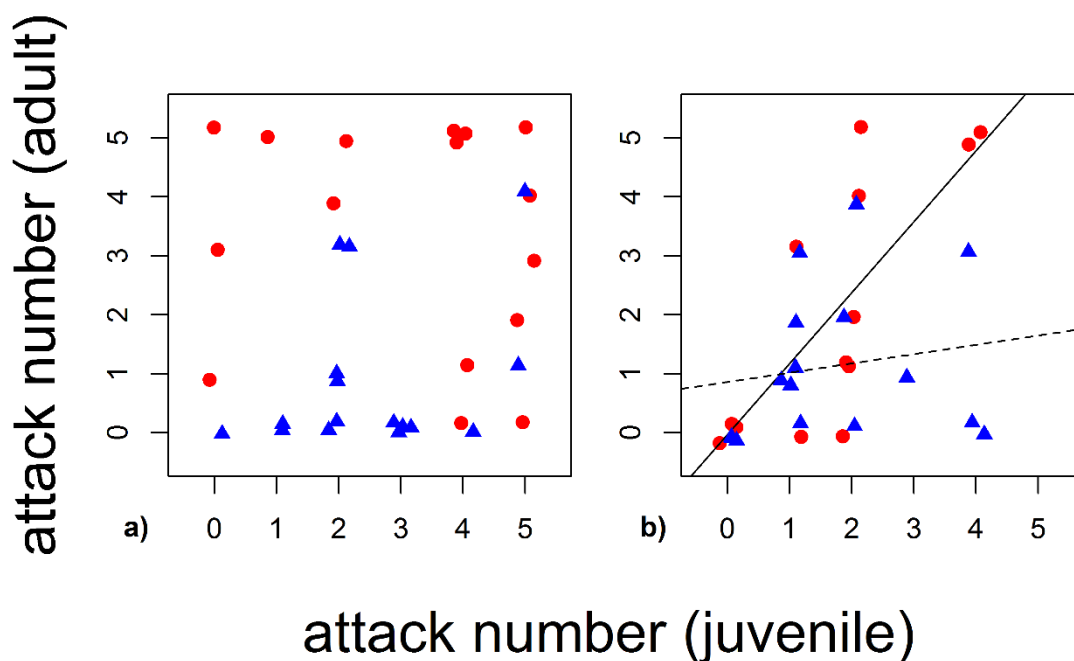
Figure 3 – Relationship between the number of attacks on a virtual prey item in juvenile and adult a) *Miomantis caffra* (male = blue triangles, female = red points), and b) *Orthodera novaezealandiae* (male =blue triangles, female = red points).

Table 1- Repeatability in aggression across sub-adult (penultimate moult) and adult life stages in two species of praying mantis.

Sex	Species	R	95% CI	p
M	*M. caffra*	0.164	0.011-0.319	0.00125
F	*M. caffra*	0.177	0.027-0.354	0.000154
M	*O. novaezealandiae*	0.15	0-0.373	0.0049
F	*O. novaezealandiae*	0.433	0.099-0.9	6.18×10^{-8}

Body mass

Body mass was not significantly different between male and female sub-adult *M. caffra* (Fig. 4; df = 98, t = 1.235, p = 0.221). However, adult female *M. caffra* were significantly heavier than adult males (df = 98, t = 10.333, p < 0.001) and sub-adult females (df = 98, t = 17.207, p < 0.001). Adult male *M. caffra* were significantly heavier than sub-adult males (df = 98, t = 3.227, p = 0.00226). For *O. novaezealandiae*, there was no significant difference between the sub-adult weights of males or females (df = 98, t = 0.569, p = 0.571). The difference in weight between adult and sub-adult male *O. novaezealandiae* was marginally

non-significant (*df* = 98, *t* = 1.920, *p* = 0.0606). Adult female *O. novaezealandiae* were

significantly heavier than adult males (*df* = 98, *t* = -4.522, *p* < 0.001) and sub-adult females

(*df* = 98, *t* = -7.005, *p* < 0.001). We also found a significant correlation between the number

of times a juvenile attacked the virtual prey item and juvenile weight in *O. novaezealandiae*

but not *M. caffra* (Fig. 5; Spearman's rank: *O. novaezealandiae*: *S* = 581.71, *rho* = 0.563, *p* =

0.00981; *M. caffra*: *S* = 5952.4, *rho* = -0.091, *p* = 0.6204).
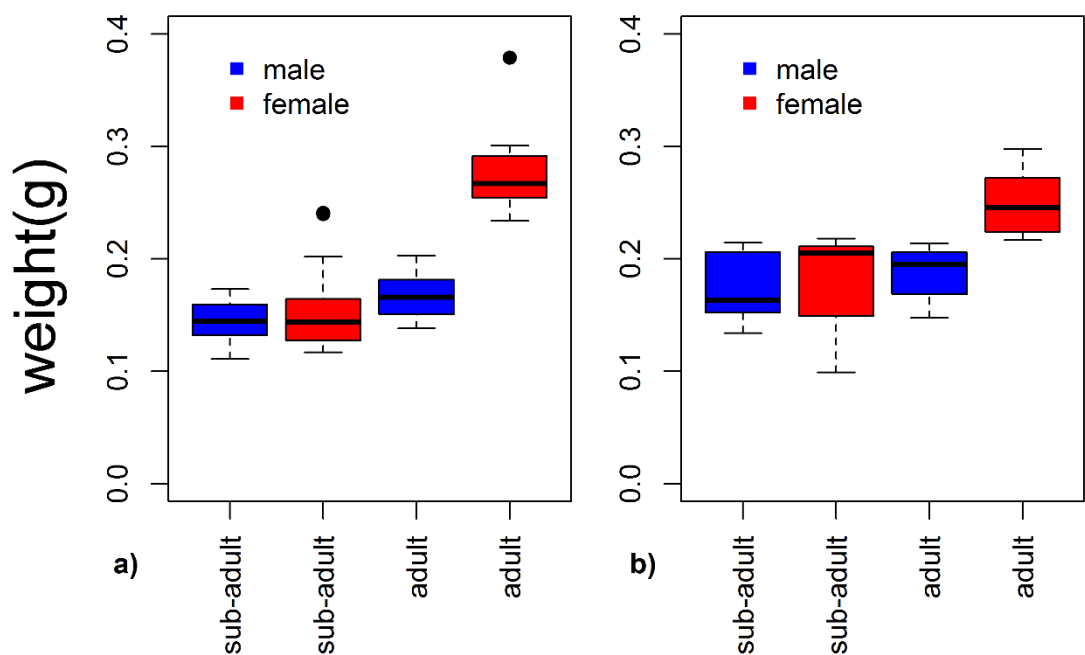
Figure 4 – Variation in weight in response to age and sex in *Miomantis caffra* (a) and
Orthodera novaezealandiae (b).
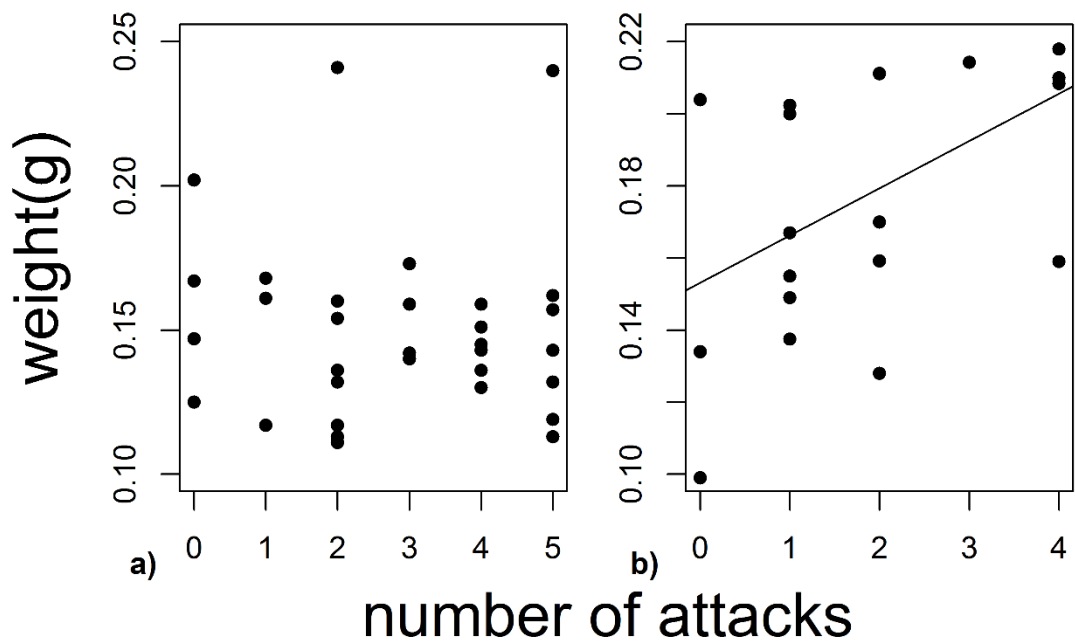
Figure 5 – The number of times a sub-adult attacks a virtual prey item is correlated with sub-adult weight in *O. novaezealandiae* (b) but not *M. caffra* (a).

Discussion

Behavioural syndromes and behavioural repeatability have previously been used to explain

the occurrence of pre-copulatory cannibalism by suggesting that cannibalism is a by-

product of strong selection for aggression towards non-conspecific prey. As a result,

aggression in individuals from species that display high rates of pre-copulatory cannibalism

should be consistent across time and environmental context. In this study, although adult

female *Miomantis caffra* were significantly more aggressive towards prey and more

cannibalistic than adult female *Orthodera novaezealandiae*, we only found evidence for

behavioural repeatability in *O. novaezealandiae*. This finding directly contradicts the

behavioural syndrome theory for pre-copulatory cannibalism. We have also shown that

male *M. caffra* can dramatically reduce their levels of aggression towards prey upon

eclosing as adults, showing that aggression can vary independently across instars in a

species where females frequently devour males prior to copulation. Moreover, we found no relationship between adult aggression and pre-copulatory cannibalism in *M. caffra*, providing further evidence that pre-copulatory cannibalism need not be a by-product of aggression towards prey. Our results suggest that behavioural syndromes are not needed to explain high levels of pre-copulatory cannibalism, even in clades where sexual cannibalism is common. It may be that the high levels of pre-copulatory cannibalism seen in some species are not a behavioural by-product, but instead have been selected for because of the direct benefits cannibalism brings to females.

Previous studies show that consistency in aggression throughout ontogeny may be linked to the presence of sexual cannibalism (Arnqvist & Henriksson, 1997; Johnson and Sih, 2005; Johnson and Sih, 2007). We found no correlation between juvenile aggression and adult aggression in *M. caffra* and very little evidence for behavioural repeatability, showing that consistency in aggression across time is not linked to the high frequency of sexual cannibalism in *M. caffra*. Previous studies have demonstrated that the individual and population-level benefits of sexual cannibalism may be highly dependent on the environment (Buskirk et al. 1984; Fisher et al. 2018). For example, sexual cannibalism may increase the incidence of virgin deaths if females continue to cannibalise males when encounters are rare, such as in sparse populations. It would therefore be advantageous for females to be able to vary how frequently they cannibalise males in response to environmental cues, such as mate availability. Previous work suggests that the presence of a behavioural syndrome lowers the plastic potential of individual behaviour (Sih et al., 2012); thus behavioural syndromes could be strongly selected against in sexually cannibalistic species to allow for greater variation in cannibalism rates.

Conversely, we found evidence for behavioural repeatability in adult female *O. novaezealandiae*, despite them being less aggressive towards prey and conspecifics than *M.*

caffra. We have also shown a positive correlation between aggression and weight in *O. novaezealandiae*, implying that consistent aggression promotes large size relative to conspecifics. Thus, behavioural consistency may be selected for to increase individual competitiveness through traits such as body size, which is likely dependent on the long-term feeding behaviour of an individual. However, there may also be a trade-off between the positive and negative fitness effects of behavioural repeatability. For example, if repeatability in aggression causes individuals to be aggressive towards potential mates, and aggression towards potential mates has negative fitness consequences, then high levels of aggression may be selected against in such species. Fitness trade-offs associated with behavioural syndromes may provide some explanation as to why female *O. novaezealandiae* are less aggressive than female *M. caffra* across all the contexts we tested.

Juvenile prey attack frequency was very similar for males and females of both species, implying that both sexes rely on high feeding rates during development to maximise their lifetime fitness and the probability of reaching adulthood. In praying mantids, males are typically the dispersing sex and therefore require functioning flight muscles and wings to locate potential mates. The development of wings and associated musculature is known to be energetically costly in other insects (Mole and Zera, 1993; Langellotto et al., 2000); thus male mantids may feed voraciously as juveniles to accommodate the energetic demands of adult dispersal. Evidence for the effect of juvenile feeding on adult dispersal is provided by the false garden mantis (*Pseudomantis albofimbriata*), where males kept on a low feeding regime as juveniles were slower at finding a mate than those that were well fed (Barry, 2013). For female mantids, adult size is likely a determinant of maximum egg production (Allen et al., 2014). In fishing spiders of the genus *Dolomedes* (family: *Pisauridae*) fixed female size (size independent of current feeding rate, i.e. cephalothorax width) was shown to significantly increase reproductive output (Spence et al. 1996; Arnqvist and Henriksson,

1997; Johnson, 2001), and was more important for determining female fecundity than adult feeding rate (Johnson, 2001). Hence it could be that the selection pressure for high juvenile aggression is similar for males and females because both sexes are equally reliant on nutrient intake to maximise adult fitness. This may be particularly true in species where males are required to develop energetically costly flight traits to allow for long distance dispersal.

Although aggression was similar for juvenile male and female *M. caffra*, adult females were significantly more aggressive than adult males. The difference in adult male and adult female aggression was due to males becoming less aggressive upon reaching adulthood, and satiating sooner. Although it is not certain why this occurs, one possibility is that males feed less as adults to limit their weight thereby allowing for easier flight dispersal. Lowering body mass increases the flight muscle to body mass ratio in flying insects and has been shown to enhance male fitness in dragonflies (Marden, 1989). Female *M. caffra* maintained their high aggression into adulthood and did not get less aggressive in response to feeding. This implies that high aggression towards prey is similarly advantageous for juvenile and adult female *M. caffra*. Because males are typically the dispersing sex in mantids, and female *M. caffra* are flightless, low body mass would not provide a fitness advantage to females. Instead, maintaining a high feeding rate may raise female fitness via increased egg production (Murphy et al. 1983; Barry et al. 2008).

In this study, high levels of adult aggression towards prey in *M. caffra* did not pre-dispose females to pre-copulatory cannibalism, implying that sexual cannibalism is not a behavioural by-product. If sexual cannibalism is not a by-product of aggression towards prey, then pre-copulatory sexual cannibalism must sometimes occur in nature because it is adaptive in itself. This could be true if males are highly nutritious for females, as has been shown in the funnel spider *Agelenopsis pennsylvanica* and the fishing spider *Dolomedes*

tenobrosus, where females that had cannibalised a male prior to copulation showed a greater number of offspring emergence (Berning et al. 2012; Schwartz et al. 2016). Similarly, in populations where males vary greatly in terms of their quality, then pre-copulatory cannibalism may be selected for as a method of mate choice (Prenter at al. 2006). In the wolf spider *Schizocosa ocreata* (family: *Lycosidae*) females are known to cannibalise smaller males over larger males (Persons and Uetz, 2005). Hence pre-copulatory cannibalism can be selected for directly and does not only occur as a by-product of selection for aggression towards prey.

If sexual cannibalism is not part of a behavioural syndrome, it is more likely that cannibalism rates will be plastic. Plasticity in cannibalism rates may be important for population persistence in a rapidly changing environment where ecological changes cause the benefits of sexual cannibalism to vary. Sexual cannibalism is far more likely to drive a population to extinction if the fitness benefits to females are low (Fisher et al. 2018), and some ecological scenarios are expected to reduce the benefits of sexual cannibalism. For example, males from degraded habitats may be smaller and less nutritious when cannibalised. In degraded habitats, males may also be less attractive, making pre-copulatory cannibalism more common, increasing the likelihood that females will die as virgins, unless they can plastically alter their cannibalistic behaviour. Similarly, degraded habitats may lead to smaller population sizes and/or lower population densities, making encounters with males less frequent (Dennis, 1989; Boukal and Berec, 2002). If females continue to devour males prior to copulation when encounters with males are rare, they will increase the incidence of virgin death in the population and could increase the risk of extinction.

Conclusions

The behavioural syndrome theory for pre-copulatory cannibalism proposes that aggression in some species is linked across developmental and ecological contexts and that sexual

cannibalism is a by-product of this aggression. Our study has shown that high rates of pre-copulatory cannibalism is not always an indication of the presence of a behavioural syndrome for aggression. Instead, sexual cannibalism may only be able to persist in some species if cannibalism rates are determined by environmental cues, not other behaviours. Secondly, we have shown that the presence of a behavioural syndrome may lead to overall lower levels of aggression in some species. This may be due to the fitness benefits of high levels of aggression being outweighed by the potential costs if aggression towards prey is correlated with aggression towards potential mates. Finally, we show that males of the sexually cannibalistic species of mantis *Miomantis caffra* can become less aggressive upon reaching adulthood, suggesting that this species can vary aggression depending on age. Our evidence supports the idea that aggression can evolve in a way that allows for variation across contexts within individuals of sexually cannibalistic species; but also that the presence of a behavioural syndrome may select for less aggressive individuals. Future work investigating the potential for sexual cannibalism rates to be plastic in response to environmental cues could be useful for conservation.

CHAPTER 5: Kin recognition mediates the effect of density and starvation on cannibalism rate

Abstract

Cannibalism is common among many invertebrate species and can have large impacts on individual fitness and population-level processes. Cannibalism has been suggested to have evolved to reduce the risk of starvation when alternative food sources are scarce. However, killing kin can substantially reduce an individual's fitness. In this study we observed the effect of genetic relatedness and population density on cannibalism rates in starved larval populations of *Drosophila simulans*. To induce starvation, larvae emerged and developed on a protein-absent food source. To manipulate relatedness, we varied the number of lineages present in a particular vial, such that a greater number of lineages meant a lower average relatedness. Density varied naturally among vials. We found that, overall, the rate of cannibalism was higher in vials where the average relatedness was lower. Additionally, there was an interaction between density and relatedness such that cannibalism rates in the non-related treatment were more positively affected by increasing density. Finally, cannibalism rates had a positive relationship with time, suggesting that prolonged starvation increases the frequency of cannibalistic behaviour. Increased cannibalism in response to starvation may promote larval survival if poor habitat quality or increased competition reduces nutrient availability. However, if genetic relatedness is high on a food patch, cannibalism may be suppressed, potentially leading to increased mortality due to starvation. By showing that cannibalism frequency in *D. simulans* is sensitive to several environmental variables, we expose the potential utility of this species as a model system for further studies into the ecology of cannibalism.

Introduction

How an organism behaves towards related individuals can have large implications for its inclusive fitness (Hamilton, 1964). As such, many species have evolved mechanisms to allow them to recognise kin and behave towards them in a way that optimises inclusive fitness. Kin recognition mechanisms rely on specific cues to assess relatedness, such as phenotypic cues that directly signal the presence of specific shared genes or genotypes (Queller et al., 2003). In addition, indirect indicators of relatedness may also be used. For example, familiarity is correlated with emergence synchrony and may be indicative of which brood an individual came from (Hopper et al., 1996; Ward & Hart, 2003). Kin recognition often facilitates the evolution of behaviours in which individuals actively help relatives survive and breed, such as in social breeding groups (Hatchwell et al., 2001; Khwaja et al., 2019). However, it is also the case in some species that kin recognition allows individuals to avoid harming or killing relatives (Pfennig et al., 1993; Pfennig et al., 1994; Dobler & Kölliker, 2009).

Cannibalism can provide a significant source of mortality and has evolved in species across many taxonomic groups, including fish (Pereira et al., 2017), amphibians (Pfenning et al., 1994), insects (Duelli, 1981; Walker & Holwell 2015) and spiders (Elgar, 1991). Cannibalism can also drive the evolution of phenotypic traits such as size variation (Elgar, 1991; Pfennig et al., 1994; Wilder & Rypstra, 2008) and can have a large impact at the population level by stabilising population fluctuations and affecting extinction risk (Ricker, 1954; Via, 1999; Fisher et al., 2018). Hypotheses for the adaptive function of cannibalism are diverse, and range from cannibalism as a foraging strategy (Barry et al., 2008; Peterson, 2010) to cannibalism as a method of mate choice (Prenter et al., 2006). With the exception of a few species of spider that can increase their paternity by being cannibalised (Andrade, 2003; Schwartz et al., 2016), cannibalism is thought to have an extremely negative effect on the fitness of the victim. As such, one would expect strong selection for individuals that can

avoid cannibalising kin, particularly in species where kin encounter rates are likely to be high. Invertebrate larvae often emerge *en masse* and thus are likely to encounter individuals from the same brood. Relatedness has been shown to play a significant role in determining cannibalism rates in the larvae of several invertebrate species including European earwigs (Dobler & Kölliker, 2009), dragonflies (Hopper et al., 1996) and spiders (Bilde & Lubin, 2001; Beavis et al., 2007). High encounter rates among siblings and the extreme fitness consequences of cannibalism make predatory invertebrate larvae ideal organisms for studying kin selection.

Fruit flies of the genus *Drosophila* have an almost ubiquitous global distribution and collectively play a major role in the decomposition of decaying organic matter. In the wild, the larvae of most *Drosophila* species typically feed on microorganisms growing on decaying vegetable matter. However, there is evidence from laboratory studies of diet switching in response to a restricted food supply. The larvae of *Drosophila melanogaster* will readily devour the carcasses of dead invertebrates when alternative food sources are absent (Ahmad et al., 2015). It has also been shown that *D. melanogaster* can increase their survival rate when starved by actively hunting and cannibalising living conspecific larvae. Moreover, the mouthparts of *D. melanogaster* develop a greater number of teeth when reared on a cannibalistic diet (Vijendravarma et al., 2013). Therefore, mouthpart plasticity in *D. melanogaster* could be an adaptation for facilitating cannibalism, as is seen in several amphibian larvae (Pfennig et al., 1994). Although cannibalism is often argued to be an artefact of crowded laboratory conditions, there is evidence that *Drosophila* larvae can be food limited in the wild (Atkinson, 1979; Grimaldi & Jaenike, 1984). In addition, the pre-existing plastic potential of *Drosophila* mouthparts implies that cannibalistic behaviour may have evolved in response to natural fluctuations in food availability.

As cannibalism can have important evolutionary and ecological impacts, understanding how the frequency of cannibalism is affected by environmental cues could be important for predicting population change. The preferential cannibalism of non-kin over kin would also provide evidence that cannibalism has been under persistent selection to promote the survival of relatives and therefore is likely to have evolved in nature as oppose to being a response to over-crowding and occasional starvation in the lab. In the current study, we observe how genetic similarity, starvation and density affects cannibalism rates in larval *Drosophila simulans*.

Methods

Rearing, treatments and measurements

Drosophila simulans is a sister species of *Drosophila melanogaster*, is globally widespread and is typically found in cosmopolitan areas. In the wild, females oviposit on patches of rotting fruit and other detritus, where larvae are likely to compete for resources (Atkinson, 1979; Grimaldi & Jaenike, 1984). Ten pre-existing *D. simulans* female isolines obtained from locations in the USA, Madagascar and Croatia were used in this study. Each isoline was established by inbreeding the offspring of a single wild caught female to produce a line of highly genetically similar individuals (David et al., 2005). Flies were kept at 22°C and reared on maize-sugar-yeast agar medium. To create the related treatment, 10 females from the same isoline were removed from the main stock and placed into individual vials to create an average relatedness among larvae of ≈ 1. In the non-related treatment, one female from each of the 10 separate isolines was taken from the main stock and placed together into individual vials to create an average relatedness of ≈ 0.1 (Figure 1). Pale colouration is an indication of a recent moult in *Drosophila*, as such, pale females were avoided for experimental selection so that only fully mature females that were likely to have mated were chosen. Females from both treatments were then given 65 hours to oviposit before being removed from the vials. In both treatments, females laid in vials containing 3ml of

the aforementioned agar medium with the yeast removed. Removing yeast is known to increase starvation and encourage cannibalism in *Drosophila melanogaster* larvae (Vijendravarma et al., 2013). Previous work on kin selection in adult Drosophila has shown that larval familiarity, i.e. whether larvae are reared in the same vials, can confound the effect of relatedness on behaviour (Hollis et al., 2015). By allocating adult females to lay in treatment vials I removed any potential confounding by familiarity, as all larvae would have emerged together regardless of whether they were in the related or non-related treatment. Additionally, unlike *D. melanogaster*, *D. simulans* females are not known to prefer the outer perimeter of a food surface over the middle (Chess & Ringo, 1985). This will likely provide consistent inter-brood familiarity due to a homogenous distribution of eggs across the food surface which would accommodate larval mixing early in development.

Isolines
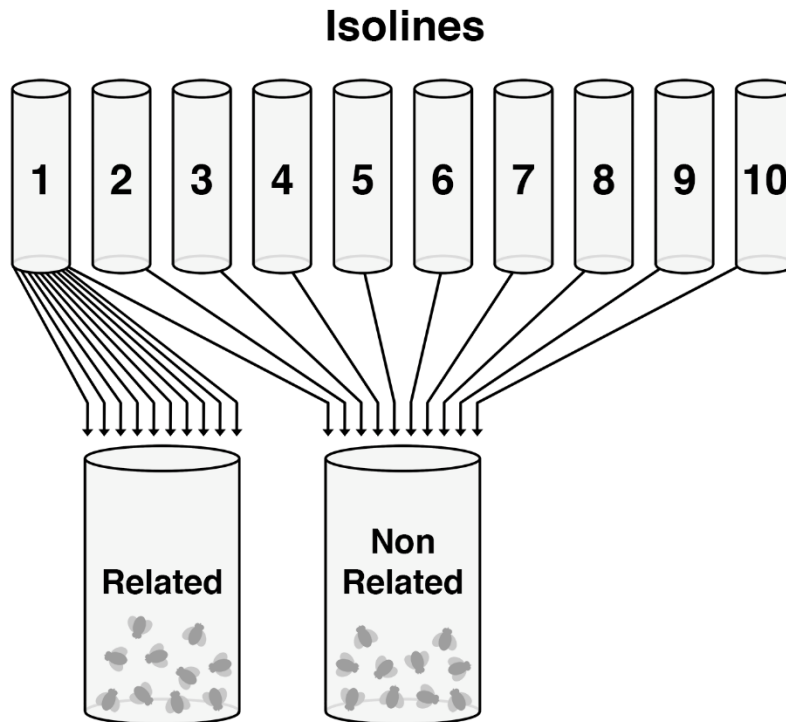
Figure 1 – Related treatments were created by allowing 10 females from a single isoline to lay eggs for 65 hours in a single vial (i.e. any related vial contained females exclusively from isoline 1,2,….. or 10). Non-related treatments were created by taking an individual female from each of the 10 isolines and allowing them to lay for 65 hours in a single vial.

After 71 hours, the food surface of each of the vials was photographed using a Canon EOS 60D attached to a Leica 1.6x magnification microscope via a custom-made microscope-SLR adapter. Magnification was kept constant throughout the experiment to ensure that the surface area being photographed remained constant. Each vial was photographed three times at ≈ 10 minute intervals; this was repeated every 24 hours. Images were then uploaded to a computer where they were analysed by eye. To get a measure of the larval density in each vial per day, the number of living larvae in each image were counted (dead larvae are identifiable by visibly necrotised tissue). Because the sclerotized mouthparts of larvae are not eaten during cannibalism (Fisher A.M., personal observations), we used the number of detached mouthparts as a measure of cannibalism rate. Vijendravarma and others (2013) found that cannibalism was more likely to occur between second (attackers) and third (victims) instar larvae, so the number of larvae that had reached 3rd instar was

also noted (see Supplementary Material for annotated example image). Photos were taken for 12 days.

Statistical analyses

The number of detached mouthparts that were counted in each vial was cumulative over time, and were thus not necessarily reflective of cannibalism rates at a particular time point. As such, we measured cannibalism for each of the related (n = 30) and non-related (n = 30) vials by taking the rate of increase in mouthparts over the 12-day experimental period. The best slope estimates were calculated using a Linear Mixed Effects Model (GLMM) that modelled mouthpart counts as a function of time (days) for each vial (see Supplementary Material for best estimates of each vial). These overall cannibalism rates were then analysed as a function of treatment (related vs unrelated), average density, the average proportion of third instars per vial, and their two-way interactions in the following linear model.

$$cannibalism\ rate \sim \left(relatedness + density + proportion\ 3^{rd}instar\right)^2.$$

Model 1

Cannibalism rates will likely depend on the larval density in a given vial. It was thus important to test for potential differences in density across the two relatedness treatments. To this end, we fitted the number of larvae (density) as a function of time, treatment, their interaction, a quadratic term for time (to test for a non-linear effect) and vial specific slope and intercept using a GLMM with Poisson error and an exponential link function.

$$density \sim treatment * time + time^2 + (vial|time).$$

Model 2

Vial-specific changes in larval density over time can be viewed in the Supplementary material. For both models, we used likelihood ratio tests to find the most parsimonious fixed effect structure. All statistics were carried out in R version 3.3.0 and GLMMs were conducted using the 'lme4' package (Bates et al., 2014).

Results

Model selection revealed that cannibalism rates in each vial are best explained by all three fixed effects (treatment, larval density, the proportion 3rd instar) as well as the interaction between density and treatment. Overall, cannibalism rate was significantly higher in vials formed of larvae from 10 different isolines (non-related vials) compared to vials where all larvae were from the same isoline (related vials) (Fig. 2: df = 55, t =9.694, p < 0.001). Overall, density had non-significant positive effect on cannibalism rates (df = 55, z = 1.491, p = 0.142). However density dependence was significantly stronger in non-related than in related vials (Fig. 3a, significant interaction, df = 55, z = 3.046, p = 0.004). Finally, the proportion of third instar larvae had a significantly positive effect on cannibalism rate (Fig. 3b: df = 55, t = 2.030, p = 0.047).
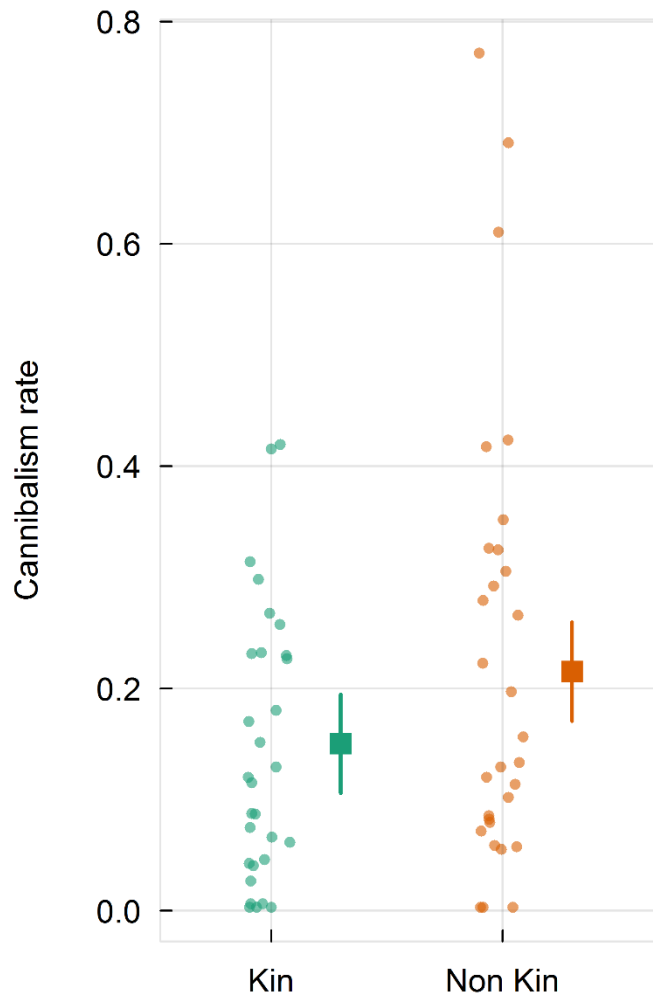
Figure 2 – Cannibalism rate is significantly higher among larval *Drosophila simulans* when surrounded by unrelated conspecifics. 95% confidence intervals used.
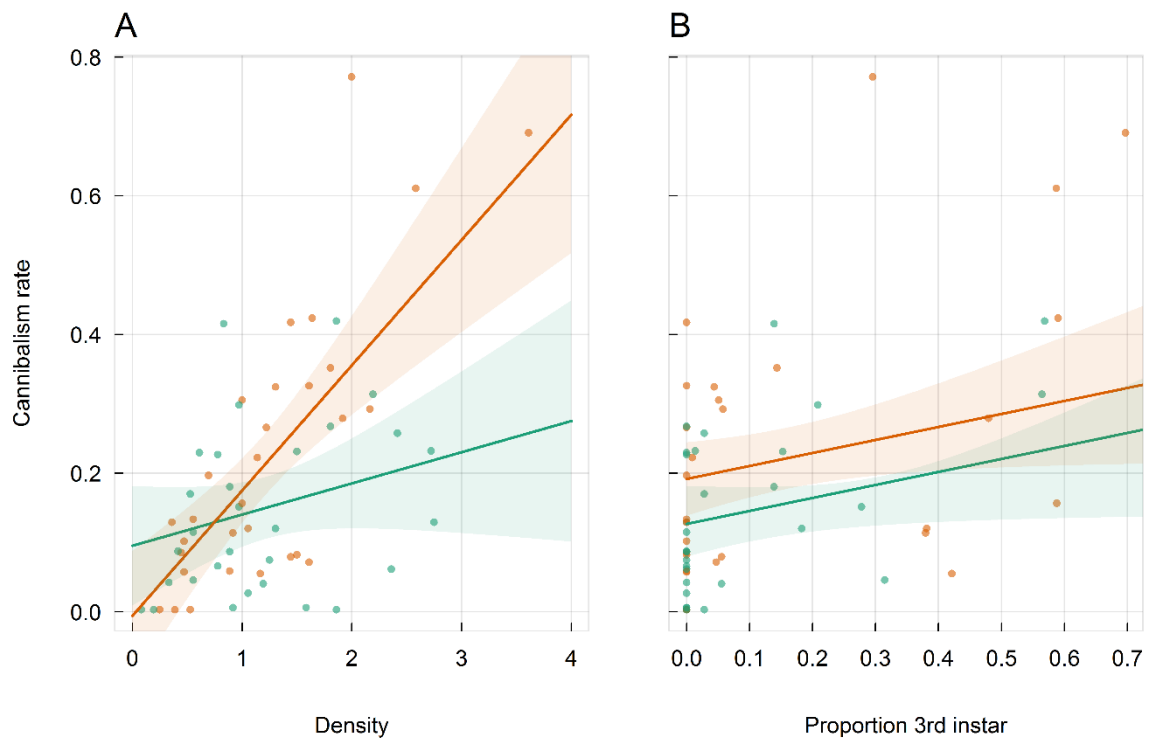
Figure 3 – Cannibalism rates among *Drosophila simulans* larvae as function of larval density and the proportion of 3rd instar. A) Density had a more positive effect on cannibalism rates among non-related (orange) larvae than related (green) larvae; B) the proportion of third instar larvae in the vial had a positive effect on cannibalism rate. 95% confidence intervals used.

Model selection on model 2 revealed that the model was most parsimonious when the effect of treatment was removed entirely suggesting that average density was not significantly different between the kin and non-kin treatments (Fig. 4a). Nor were there treatment-specific effects on density over time. However, the minimal adequate model detected a significant non-linear decrease in larval density over time (Fig. 4b: $df = 57$, $t = -12.871$, $p < 0.001$).
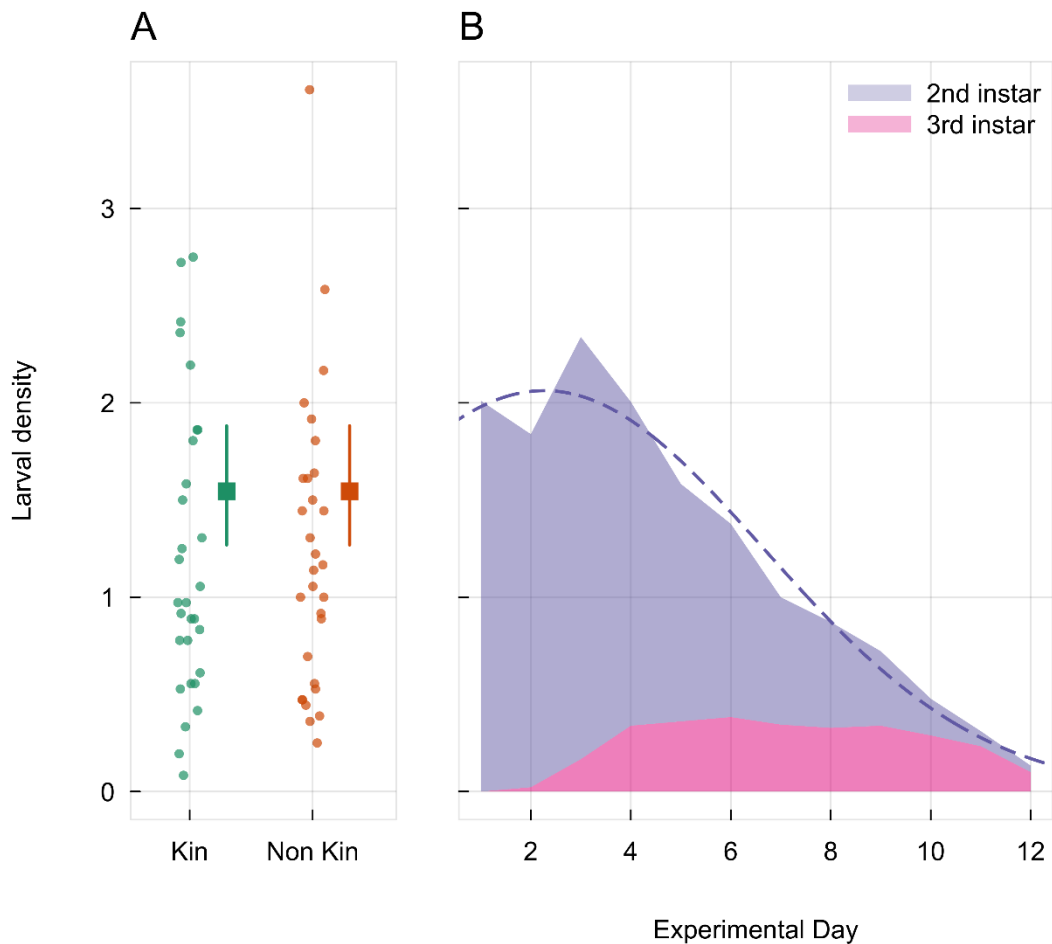
Figure 4 – Variation in larval density in vials containing *Drosohila simulans*. A) No significant difference in density between relatedness treatments (95% confidence intervals). B) Larval density decreased significantly over time.

Discussion

In this study we provide evidence for direct kin selection in *D. simulans* by showing that

cannibalism rates are reduced in the presence of highly related individuals even after

controlling for familiarity. We have also shown that density, a major driver of cannibalism

in other species, has a stronger positive effect on cannibalism rates among non-related

individuals than related individuals. Cannibalism rates had a positive linear relationship

with time despite a reduction in density over time. This implies that hunting effort may

increase in response to prolonged starvation. Finally, we have shown that the ratio of third

to second instar larvae in a vial has a positive effect on cannibalism rate. This indicates that

high rates of cannibalism may be able to reduce development time under nutritional stress, or that cannibalism is more likely to occur between third and second instar larvae.

Species vary in how they assess relatedness. In some cases, indirect measures of relatedness are used to approximate which individuals are kin. For example, there is evidence from several fish species that suggests individuals which are reared together tend to form shoals, thus association with kin is a by-product of close proximity during early lifestages (Griffiths & Magurran, 1999; Ward & Hart, 2003). Alternatively, some species directly asses their relatedness to other individuals by detecting phenotypic traits that are strongly linked to specific genes or genotypes (Keller & Ross, 1998; Lizé et al., 2006). In this study, we controlled for differences in familiarity across treatments by ensuring that larvae in both the kin and non-kin treatments emerged together (see Methods). As such, it appears that *D. simulans* larvae are able to directly assess relatedness using genetically-linked phenotypic cues. Being able to directly assess relatedness may be important for species that are likely to encounter a mixture of related and non-related individuals early in their lifecycle. In the wild, *Drosophila* larvae feed on spatially discrete food patches where the average relatedness is likely to be determined by the number of females that have oviposited on a particular patch. Lab evidence suggests that female *Drosophila simulans* avoid food patches already populated by conspecific eggs or larvae (Chess & Ringo, 1985). Despite this preference, females of various wild-caught *Drosophila* species, including *D. simulans*, will lay on substrate shared with other non-related females. A female's selection criteria for oviposition sites may therefore be dependent on the level of competition, such that previously occupied sites are accepted if vacant sites are scarce due to higher female density. Thus, environmental fluctuations may influence the average genetic relatedness on food patches, selecting for larvae that can use kin recognition to behave optimally under a range of scenarios affecting relatedness.

Cannibalism rate is known to increase with population density in several groups including insects (Hopper, 1996; Via, 1999), fishes (Giles et al., 1986; Klug et al., 2007; Pereira et al., 2017) and amphibians (Wildy et al., 2001; Pizzatto & Shine, 2008). Increased cannibalism rates in response to high densities could have evolved as a means of reducing competition for food, or it may simply be that opportunities to cannibalise are greater at high densities. In this study we found that density had a stronger positive effect on cannibalism rate in the non-related treatment group. This implies that, on average, the fitness benefits of cannibalising at high densities are smaller than the costs associated with killing kin in *D. simulans*. However, there may be certain scenarios in which a lack of kin cannibalism in response to high densities of related offspring creates an evolutionary trap in which individuals behave in a way that is maladaptive. For example, because smaller food patches are less able to sustain multiple *Drosophila* broods, fewer females are likely to oviposit on small patches (Chess & Ringo, 1985). Therefore, smaller food patches are likely to be associated with higher relatedness. Whereas density-induced nutritional stress due on larger patches may be partially offset by opportunities to cannibalise non-related individuals, the suppression of cannibalism on small patches may lead to higher levels of starvation. However, there is evidence to suggest that larval density decreases with patch size in both *D. melanogaster* and *D. simulans* (Mitsui & Kimura, 2000). As such, females may have evolved mechanisms to avoid frequent oviposition on small patches so that food patches populated almost exclusively by kin do not experience high densities.

In any instance of cannibalism, the predator is likely to receive some amount of nutritional benefit, which may be particularly true when individuals are starved. For some species, cannibalism can significantly increase fitness by reducing development time (Michaud, 2003), increasing survival (Yashuda & Ohnuma, 1999) and/or increasing fecundity (Schwartz et al., 2016). In the current study, we found that vials in which a higher proportion of larvae reached the third instar were associated with higher rates of

cannibalism. This could suggest that, under nutritional stress, cannibalism increases survival allowing individuals to reach a later stage of development. In the only other paper to formally report predatory cannibalism in fruit fly larvae, Vijendravarma and others (2012) found that survival rates in starved *Drosophila melanogaster* larvae increased with cannibalism rate. Thus both studies suggest that one of the adaptive properties of cannibalism in *Drosophila* is likely to be protection against starvation. However, because we did not directly observe and compare cannibalism rates among second instars and between second and third instars, we cannot say whether increased cannibalism promotes faster development, or whether development asynchrony promotes cannibalism. Nevertheless, Vijendravarma and others (2012) showed that increased cannibalism between second and thirds instars was due the presence of late 'wandering stage' third instars, which are fairly sedentary and therefore more vulnerable to cannibalism. Because of the short timeframe of the current study, none of the larvae reached the 'wandering phase' before the 12 days of observation were over. Hence it is likely that the faster development times seen in this study were a product of high cannibalism rates, not the other way around.

In the current study, cannibalism often had a positive linear relationship with time, despite density having a negative relationship with time (see supplementary material). This means that cannibalism rates can be maintained, even if fewer potential victims are present. It may be that *D. simulans* larvae are more willing to cannibalise conspecifics they encounter or are increasing their hunting effort in response to prolonged starvation. A similar positive relationship between time spent starved and cannibalism frequency has been observed in juvenile wolf spiders (Samu et al., 1999; Peterson et al., 2010). Demonstrating a continuous relationship between starvation and cannibalism implies that cannibalism rates are flexible with regards to the environment as oppose to being a behaviour that is simply turned on or off in response to an environmental threshold. Cannibalism rates that are highly plastic in

response to environmental cues may have evolved to allow individuals to behave in a way that is optimal for fitness and promote survival across a range of varying habitats (Sih et al., 2011).

Our study is the first to observe the effect of relatedness on predatory cannibalism in *Drosophila*. We have shown that the cannibalism of non-kin is preferred over the cannibalism of kin, and that high levels of relatedness is likely to be assessed directly using genetically-linked phenotypic traits. The fact that the isolines used in this study were not exposed to non-related individuals prior to these experiments suggests that cannibalism evolves naturally in response to fluctuating levels of relatedness in the wild, and is not merely an artefact of laboratory conditions. We also show that relatedness reduces the likelihood that individuals will engage in cannibalistic behaviour when conspecific density is high. This could create an evolutionary trap in which related larvae cannot mitigate the effect of increased competition for food in high density scenarios. We think that future work should aim to analyse cannibalism across a range of different *Drosophila* species with the aim of establishing a link between species ecology and kin recognition.
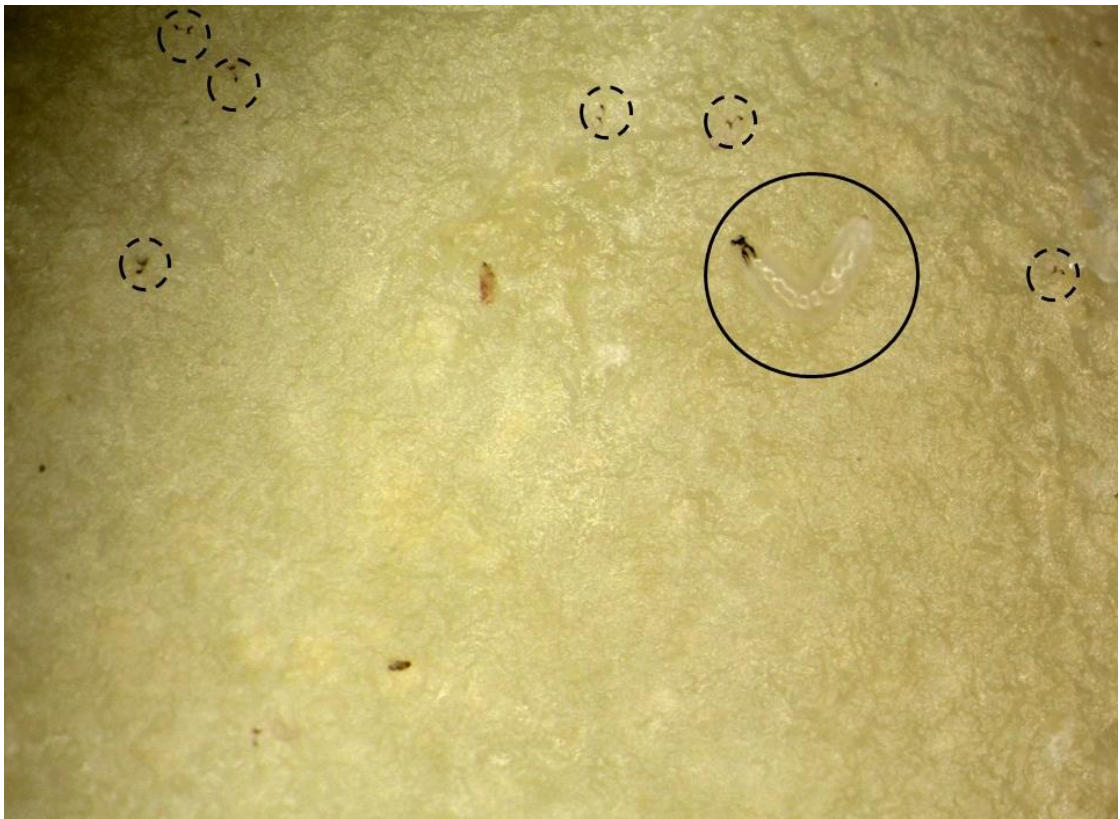
Figure S1 — An example data image showing a third instar larvae (solid-line circle) and detached mouthparts (dashed-line circles).
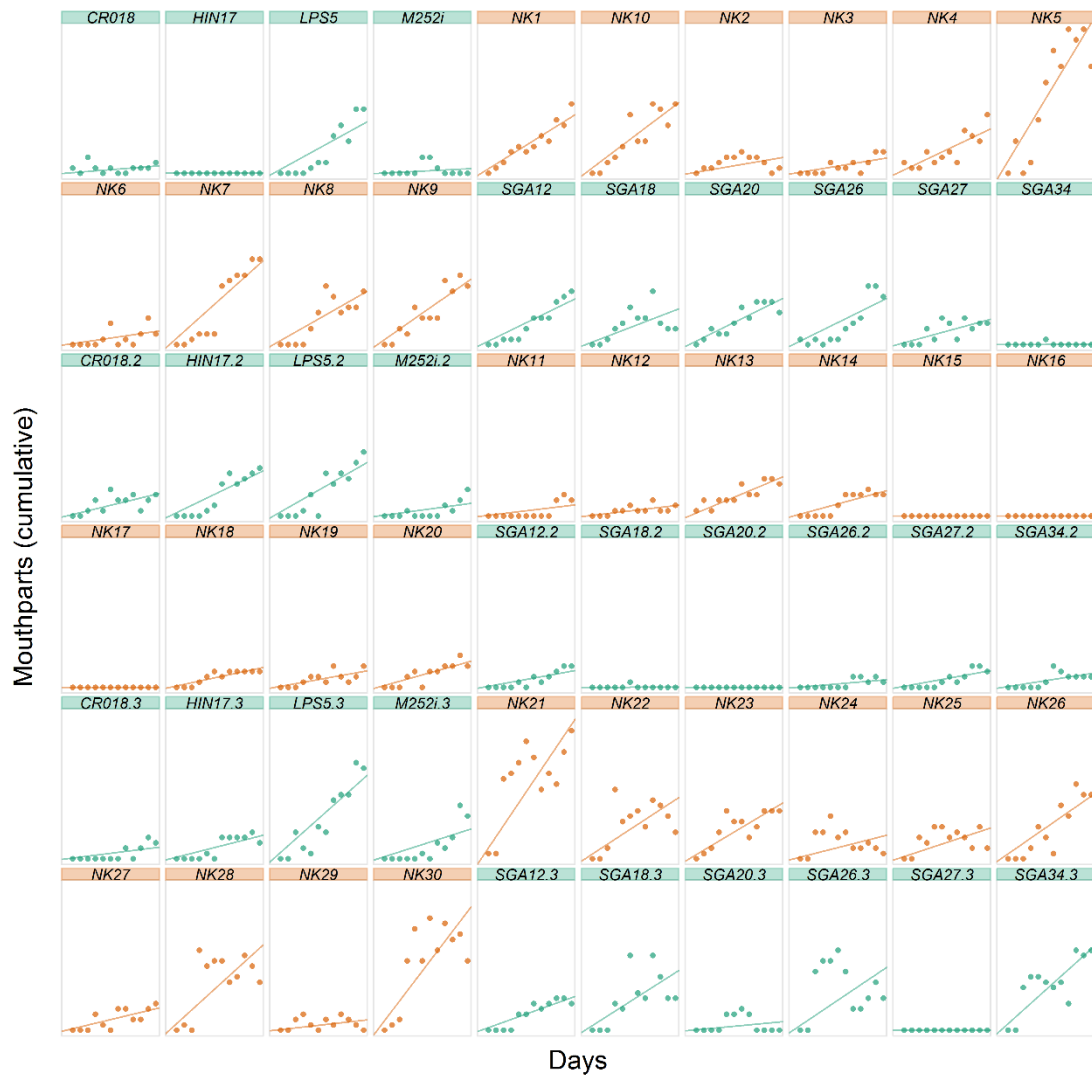
Figure S2 – Vial-specific variation in the number of detached mouthparts counted for each of the 12 experimental days in vials containing related (green) or non-related (orange) *Drosophila simulans* larvae.
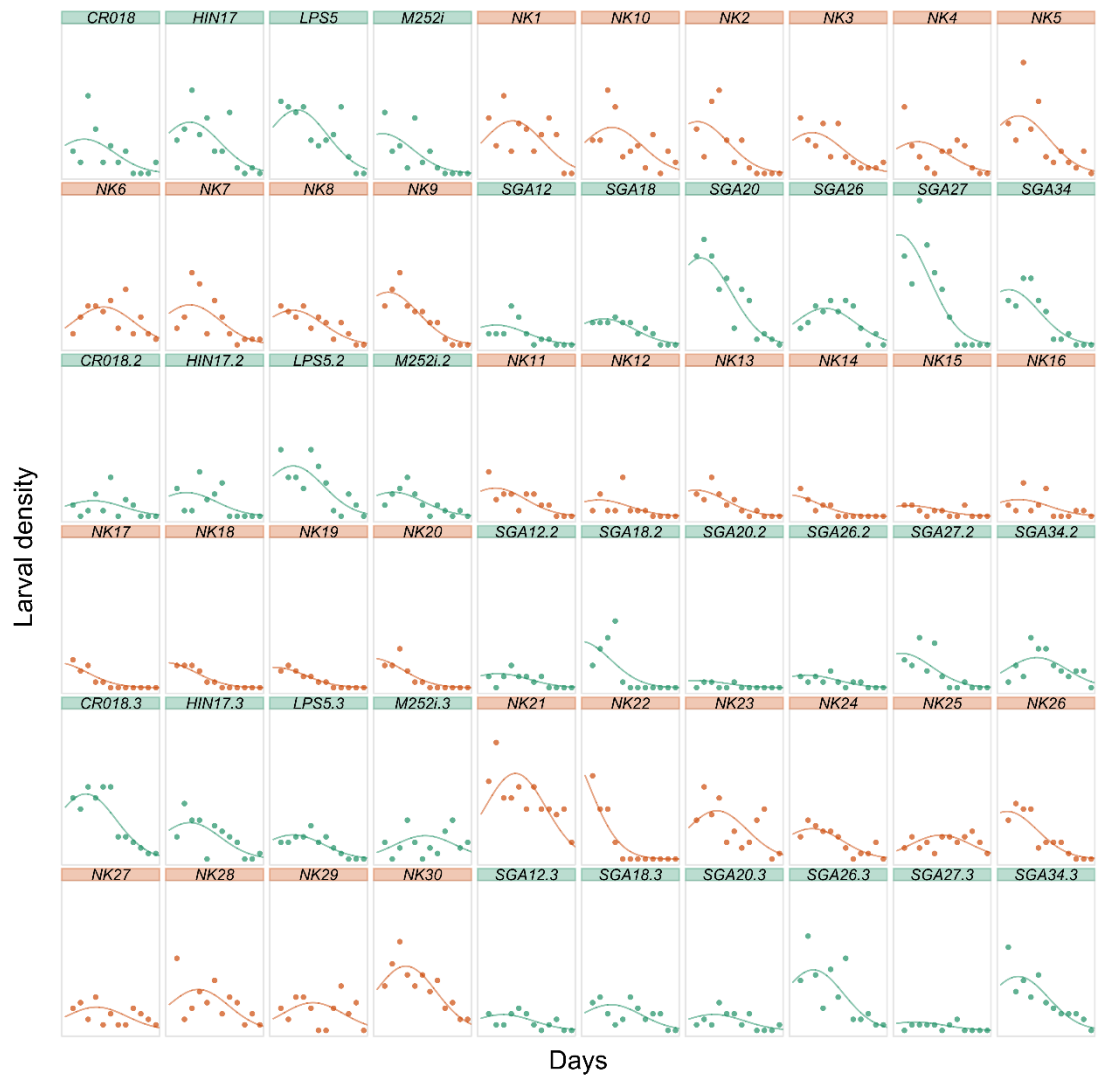
Figure S3 – Vial-specific variation in larval density in response to time (12 days) for vials containing related (green) and non-related (orange) *Drosophila simulans* larvae.

GENERAL DISCUSSION

The over-arching question that motivated this PhD was "do some reproductive behaviours become maladaptive under certain environmental conditions?". The appeal of this question came from the fact that ecologists and conservationists often overlook the ecological impacts of subtle behaviours that are not easily observable in the wild and are specific to particular groups or species. This presented me with the opportunity to do research in a field of biology in which it is easy to come up with novel and potentially important questions. The thesis mainly focuses on sexual cannibalism, this is in part due to the fact that sexual cannibalism is common in spiders and mantids, two animal groups I find particularly interesting. Also, sexual cannibalism has the potential to inflict large fitness costs on both males and females, and I strongly felt that these costs could manifest themselves at the population-level given the right ecological conditions.

When writing the original project outline that was used for the bid for NERC funding, I realised that in order to directly observe the populations level effects of a behaviour in the wild, I would likely need to monitor several populations over a prolonged time period. This would have been outside the scope of a PhD timeframe and did not seem feasible. As such, I decided to incorporate a substantial theoretical component, which would allow me to estimate the population-level effects of sexual cannibalism over many generations and under many ecological scenarios. One of the assumptions that runs through the models created in this PhD is that behaviours are not plastic with regards to the environment. However, plasticity is known to play a major role in determining how robust individuals are to a rapidly changing environment (Sih et al., 2011). Thus determining the plasticity of sexual cannibalism may be important for the conservation of predatory invertebrates. Therefore, I allocated about three quarters of my time during the PhD to observing animal behaviour in the lab under conditions designed to test for behavioural plasticity. As is probably the case with many projects, the PhD came to an end before I felt like I had asked

all of the questions I wanted to. For the remainder of this discussion, I summarise the questions that I feel I have answered, and outline how I would continue the work given the opportunity.

Theoretical findings

There are several theoretical studies that predict the circumstances under which cannibalism is likely to evolve. However, at the time of writing, there is no published literature (other than chapter 1 of this thesis) that explicitly investigates the ecological impacts of sexual cannibalism. As such, chapter one begins to fill this gap by observing the impact of sexual cannibalism on population viability. Two modelling methods, a deterministic and a stochastic model, were used to increase the reliability of the findings. Both models produced very similar results to make for a convincing argument for the population impact of sexual cannibalism. There were three main results that were of greatest interest. Firstly, we found that sexual cannibalism has a 'hump-shaped' relationship with population growth rate, such that intermediate rates of cannibalism gave the highest population growth rates. Secondly, high rates of pre-copulatory cannibalism are particularly likely to cause extinction. Third, we found that the population-level effects of sexual cannibalism were highly dependent on the amount of fecundity benefit a female could receive by cannibalising a male. Specifically, population growth rate was lower when males were less nutritious. This is likely to have ecological relevance if the nutritional value of males changes with the environment, i.e. if males are smaller in habitats of poor quality. Moreover, if females become more cannibalistic due to food shortages in a poor quality habitat, this may raise cannibalism rates to a level that is detrimental for the probability of population persistence.

Although my first chapter produced novel and interesting results, it did not address how the ecological effects of sexual cannibalism change in response to mate availability. In my opinion, this should be a fundamental question that biologists ask of any mating system in

which females may rely on access to multiple males in order to ensure reproduction.

Therefore, my second chapter forms a logical continuation of chapter 1 and focuses on the potential Allee effects associated with sexually cannibalistic mating systems. For chapter 2, an individual-based model was used instead of a deterministic model or a stochastic simulation. This was because any fecundity benefits associated with pre-copulatory cannibalism would only be received by the female if she went on to mate with another male. Thus we needed to continuously monitor each individual female such that any previous instances of cannibalism were taken into account when determining fecundity. Individual-based models are also argued to be more true to nature, particularly when dealing with small populations (DeAngelis & Mooji, 2005). The first finding of this study was that mate-finding rate had a negative sigmoidal relationship with extinction risk, this was true whether the type of cannibalism was pre- or post-copulatory. This has two important implications: firstly, it shows that low mate-finding rate can cause extinction; second, it shows that extinction rate can increase or decrease rapidly over a short range of mate-encounter rates, creating an extinction 'threshold'. Another interesting and slightly counterintuitive finding of this study was that post-copulatory cannibalism can reduce extinction risk, if the female gains nutrition from eating the male and thereby produces more offspring. As such, post-copulatory cannibalism may be beneficial for reducing extinction risk in small or sparse populations if males are nutritious.

The models produced during my PhD make a start at filling some of the gaps in the sexual cannibalism literature. However, I think there are many interesting unanswered questions related to the ecological and evolutionary impacts of sexual cannibalism that deserve attention. To continue on from the theoretical work of my PhD, I would build an evolutionary model that looks at how population size and density alter the selection pressures acting on cannibalistic individuals. This would provide insights into how cannibalistic species might adapt to changing environments over evolutionary timescales.

Furthermore, it would also be interesting to investigate how population sizes experienced by organisms in their recent evolutionary history affects their ability to cope with rapid environmental change. Another potential continuation of my work, which was actually suggested by a reviewer, would be to look at how the operational sex ratio affects the population-level effects of sexual cannibalism. It could be that male-biased sex ratios reduce the likelihood of cannibalistic species going extinct due to low mate availability. Also, although male-biased sex ratios are not known to occur in praying mantids, they are known to be fairly common in some sexually cannibalistic spiders (Schneider & Elgar, 2001; Zimmer et al., 2012). Thus establishing a link between sex ratio and extinction risk in sexually cannibalistic species could provide insights into why male-biased sex ratios persist in nature. Finally, I would have also liked to investigate the evolutionary implications of behavioural syndromes and their role in maintaining phenotypic diversity in sexually cannibalistic populations. Other studies have shown that aggression in sexually cannibalistic individuals may be linked across contexts, such that females which are aggressive towards potential mates may also be aggressive towards other females. This may lead to the occurrence of potentially costly female-female competition. For example, if aggressive females fight when they encounter one another, leading to significant harm or death, then the benefits of aggression may be dependent upon the frequency of other aggressive females. As such, the frequency of aggressive individuals may vary over time, preserving phenotypic diversity in the population.

Experimental findings

As mentioned earlier, the theoretical methods used in my PhD make the assumption that sexual cannibalism rates are not plastic in response to certain environmental parameters such as mate density. However, female behavioural plasticity could, to some extent, mitigate the negative effects certain environmental scenarios inflict on cannibalistic species. The first lab experiments I conducted during my PhD attempted to alter the

female's perception of the density of males in the environment and observe whether this affected aggression towards males. To do this I exposed adult female *Dolomedes fimbriatus* (a species that has previously been shown to be highly aggressive (Arnqvist, 1992)) to different males in succession. I predicted that perceived density would increase in response to an increased number of encounters and lead to increased aggression. Surprisingly, attack rates in the *D. fimbriatus* that I collected were very low, going against the current perception that female *Dolomedes spp.* are highly aggressive towards males (Johnson & Sih, 2005; Schwartz et al., 2016). I also found that the number of males the female had previously been exposed to had no effect on the probability she would attack a male. The only significant result from this study was that courtship effort (measured using latency to begin courting) in males was lower during their second encounter with a female when compared to their first. This implies that males have not evolved to perform consistently energetic courtship behaviours, which may be due to a low likelihood of remating, something that is thought to be fairly common in male spiders (Andrade, 2003; Nessler et al., 2006). In my opinion, the most interesting finding of this study was that females would lay and guard unfertilised egg cases and cease to be attractive to males. This may significantly reduce the reproductive timeframe of the female, which may be detrimental to female fitness in sparse populations where females may have to wait longer before encountering a male. The *Dolomedes* study did not yield as large a sample size as I would have liked, this is mainly due to the fact that it was difficult to get permission from Natural England to collect enough spiders. However, I do feel like the data collected forms a solid preliminary study and provides some novel insights into the reproductive behaviour of *D. fimbriatus*.

Behavioural syndromes can be defined as correlations between the same behaviour across different contexts, or correlations between different behaviours. Behavioural syndromes can reduce behavioural plasticity (Sih et al., 2012) and are thought to be responsible for the

occurrence of pre-copulatory cannibalism in some species (Arnqvist & Henriksson, 1997; Johnson & Sih, 2005). The data collection for my second experimental chapter took place in New Zealand over two field seasons. I observed juvenile and adult aggression towards prey and aggression towards conspecific males in two species of praying mantis, *Miomantis caffra* and *Orthodera novaezealandiae*. Prior to my study, it was already known that female *M. caffra* frequently consumed males prior to copulation, and that *O. novaezealandiae* was far less cannibalistic. As such, I expected to find evidence of a behavioural syndrome for aggression in *M. caffra* but not *O. novaezealandiae*. Surprisingly, although *M. caffra* was more aggressive towards prey and conspecific males than *O. novaezealandiae*, no evidence for a behavioural syndrome was found. However, we did find evidence for a behavioural syndrome in *O. novaezealandiae*, where aggression towards prey was correlated across lifestages in females. This result suggests that pre-copulatory cannibalism need not be part of a behavioural syndrome, but may be selected for directly due to its adaptive properties. Because behavioural syndromes are often linked to a lack of behavioural plasticity, my study provides indirect evidence that pre-copulatory cannibalism in *M. caffra* is plastic. Given more time, I would like to confirm whether sexual cannibalism in *M. caffra* really is plastic by directly testing cannibalism rates in response to different environmental scenarios.

My final experimental chapter observed how genetic relatedness and density affected cannibalism in larval *Drosophila simulans*. It has previously been shown in several taxa that there is selection for individuals to avoid cannibalising siblings (Loekle et al., 1982; Pfennig & Collins, 1993; Dobler & Kölliker, 2009). It has also been shown that high densities are more likely to be conducive of cannibalism. Therefore, I predicted that cannibalism rates would be higher when genetic relatedness was lower, and that higher density would lead to higher cannibalism rates. Both of these predictions were shown to be correct. Moreover, we controlled for familiarity across treatments, implying that relatedness is determined

using phenotypic cues that are associated with specific genes or genotypes. Discovering a link between high density and cannibalism rate also gives the study ecological relevance, as cannibalism has previously been shown to have a stabilising effect on population dynamics at high density. Also, relaxed cannibalism rates at low densities may prevent populations from suffering from Allee effects. Once again there were other questions I would have liked to have asked with regards to cannibalism in *Drosophila*. Mainly, I would like to have tested cannibalism across a suite of phylogenetically distinct species and attempt to make a link between ecology and cannibalism. Specifically, I think that there is likely to be an effect of polyandry on cannibalism, with larvae from more polyandrous species being more cannibalistic due to lower within-brood relatedness. It may also be that larvae from polyandrous species may be less likely to have evolved kin recognition mechanisms due to a lower chance of encountering kin. Although there are other studies that have observed kin effects on cannibalism rates in juveniles, I am unaware of any studies that have tested the effect of relatedness on sexual cannibalism rates. It would be interesting to test for a link between species ecology and the strength of selection for kin recognition in sexually cannibalistic species. For example, if a species is highly dispersive, individuals may be less likely to encounter kin as adults; as such, highly dispersive individuals may be less likely to be able to recognise kin.

Conclusions

As mentioned earlier, sexual cannibalism is just one reproductive behaviour in which the population level effects are highly dependent on the environment, but there are likely to be many more. Any species in which females are highly reliant on substantial supply of males could be at an increased risk of extinction if the supply of males is rapidly reduced. Especially if female behaviour is not plastic in response to sudden reductions in mate availability. For example, in systems where females are particularly choosy and regularly reject males are more likely to reject all of the males they encounter if males are rare. A

similar argument can be made for cases in which the frequency of male sterility is high, where females will be more likely to mate with only sterile males if they mate with fewer males in total. Aside from increased difficulty in finding a mate, there are examples of how various other behaviours may reduce population viability in the face of rapid environmental change. For example, female lesser-spotted woodpeckers (*Dendrocopos minor*) commonly abandon the nest during the 'late-chick' period leaving the male to care for the offspring alone (Rossaminth et al., 2009; Charman et al., 2012). Provisioning rates from a single parent may be adequate for ensuring chick survival in habitats where invertebrate abundance is high, but this may not be the case if food resources become scarce. Thus, it may be that *D. minor* populations are particularly sensitive to decline in impoverished habitats (Charman et al., 2012). There are several examples of work that attempts to identify how certain behaviours that were adaptive for an organism in their recent evolutionary history may reduce individual fitness and population viability in a changing environment (Schlaepfer et al., 2002). However, at the time of writing, the field of conservation behaviour is still young. As such, there are still many unanswered questions regarding how the ecological impact of behaviours interacts with the environment. Hopefully this thesis has managed shine some light on the conservation value of studying animal behaviour.

REFERENCES

Ahmad, M., Chaudhary, S.U., Afzal, A.J. and Tariq, M., 2015. Starvation-induced dietary behaviour in *Drosophila melanogaster* larvae and adults. *Scientific reports*, *5*, p.14285.

Allen, L.E., Barry, K.L. and Holwell, G.I., 2014. Different paths to sexual size dimorphism in two praying mantids, *Pseudomantis albofimbriata* and *Hierodula majuscula*. *Insect science*, *21*(2), pp.227-233.

Andrade, M.C., 1996. Sexual selection for male sacrifice in the Australian redback spider. *Science*, *271*(5245), pp.70-72.

Andrade, M.C., 2003. Risky mate search and male self-sacrifice in redback spiders. *Behavioral Ecology*, *14*(4), pp.531-538.

Andren, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, pp.355-366.

Angulo, E., Roemer, G.W., Berec, L., Gascoigne, J. and Courchamp, F., 2007. Double Allee effects and extinction in the island fox. *Conservation Biology*, *21*(4), 1082-1091.

Agarwala, B.K. and Dixon, A.F., 1993. Kin recognition: egg and larval cannibalism in *Adalia bipunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology*, *90*(1), pp.45-50.

Anthony, L. L., & Blumstein, D. T., 2000. Integrating behaviour into wildlife conservation: The multiple ways that behaviour can reduce N_e. *Biological Conservation*, *95*(3), 303– 315.

Arnqvist, G., 1992. Courtship behavior and sexual cannibalism in the semi-aquatic fishing spider, *Dolomedes fimbriatus* (Clerck)(Araneae: Pisauridae). *Journal of Arachnology*, *20*(3), pp.222-226.

Arnqvist, G., & Henriksson, S., 1997. Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. *Evolutionary Ecology*, *11*(3), pp.255– 273.

Atkinson, W.D., 1979. A field investigation of larval competition in domestic Drosophila. *The Journal of Animal Ecology*, pp.91-102.

Baras, E., Ndao, M., Maxi, M.Y.J., Jeandrain, D., Thomé, J.P., Vanadewalle, P. and Mélard, C., 2000. Sibling cannibalism in dorada under experimental conditions. I. Ontogeny, dynamics, bioenergetics of cannibalism and prey size selectivity. *Journal of Fish Biology*, *57*(4), pp.1001-1020.

Barry, K.L., Holwell, G.I. and Herberstein, M.E., 2008. Female praying mantids use sexual cannibalism as a foraging strategy to increase fecundity. *Behavioral Ecology*, *19*(4), pp.710-715.

Barry, K.L., 2010. Influence of female nutritional status on mating dynamics in a sexually cannibalistic praying mantid. *Animal Behaviour*, *80*(3), pp.405-411.

Barry, K.L., Holwell, G.I. and Herberstein, M.E., 2009. Male mating behaviour reduces the risk of sexual cannibalism in an Australian praying mantid. *Journal of Ethology*, *27*(3), pp.377-383.

Barry, K.L., Holwell, G.I. and Herberstein, M.E., 2010. Multimodal mate assessment by male praying mantids in a sexually cannibalistic mating system. *Animal Behaviour*, *79*(5), pp.1165-1172.

Barry, K.L. and Kokko, H., 2010. Male mate choice: why sequential choice can make its evolution difficult. *Animal Behaviour*, *80*(1), pp.163-169.

Barry, K.L., 2013. You are what you eat: food limitation affects reproductive fitness in a sexually cannibalistic praying mantid. *PLoS One*, *8*(10), p.e78164.

Baruffaldi, L. and Andrade, M.C., 2015. Contact pheromones mediate male preference in black widow spiders: avoidance of hungry sexual cannibals? *Animal Behaviour*, *102*, pp.25-32.

Bates D., Maechler M., Bolker B., Walker S., 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), pp.1-48.

Bartos, M. and Minias, P., 2016. Visual cues used in directing predatory strikes by the jumping spider *Yllenus arenarius* (Araneae, Salticidae). *Animal behaviour*, *120*, pp.51-59.

Beavis, A.S., Rowell, D.M. and Evans, T., 2007. Cannibalism and kin recognition in *Delena cancerides* (Araneae: Sparassidae), a social huntsman spider. *Journal of Zoology*, *271*(2), pp.233-237.

Bell, A.M., Hankison, S.J. and Laskowski, K.L., 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, *77*(4), pp.771-783.

Berec, L., Kramer, A.M., Bernhauerová, V. and Drake, J.M., 2018. Density-dependent selection on mate search and evolution of Allee effects. *Journal of Animal Ecology*, *87*(1), pp.24-35.

Berning, A. W., Gadd, R. D., Sweeney, K., MacDonald, L., Eng, R. Y., Hess, Z. L., & Pruitt, J. N., 2012. Sexual cannibalism is associated with female behavioural type, hunger state and increased hatching success. *Animal Behaviour*, *84*(3), pp.715– 721.

Bilde, T. and Lubin, Y., 2001. Kin recognition and cannibalism in a subsocial spider. *Journal of Evolutionary Biology*, *14*(6), pp.959-966.

Birkhead, T. R., Lee, K. E., & Young, P., 1988. Sexual cannibalism in the praying mantis *Hierodula membranacea*. *Behaviour*, *106*(1), pp.112– 118.

Blanckenhorn, W.U., Mühlhäuser, C., Morf, C., Reusch, T. and Reuter, M., 2000. Female choice, female reluctance to mate and sexual selection on body size in the dung fly *Sepsis cynipsea*. *Ethology*, *106*(7), pp.577-593.

Blumer, L.S., 1979. Male parental care in the bony fishes. *The Quarterly Review of Biology*, *54*(2), pp.149-161.

Blumstein, D. T., 1998. Female preferences and effective population size. *Animal Conservation*, *1*(3), pp.173– 177.

Bose, A.P., Lau, M.J., Cogliati, K.M., Neff, B. and Balshine, S., 2019. Cannibalism of young is related to low paternity and nest take-overs in an intertidal fish. *Animal Behaviour*, *153*, pp.41-48.

Boukal, D.S. and Berec, L., 2002. Single-species models of the Allee effect: extinction boundaries, sex ratios and mate encounters. *Journal of Theoretical Biology*, *218*(3), pp.375-394.

Brown, W.D., Muntz, G.A. and Ladowski, A.J., 2012. Low mate encounter rate increases male risk taking in a sexually cannibalistic praying mantis. *PLoS One*, *7*(4), p.e35377.

Brown, W. D., & Barry, K. L., 2016. Sexual cannibalism increases male material investment in offspring: Quantifying terminal reproductive effort in a praying mantis. *Proceedings of the Royal Society B*, *283*(1833), 20160656.

Buskirk, R. E., Frohlich, C., & Ross, K. G., 1984. The natural selection of sexual cannibalism. *The American Naturalist*, *123*(5), pp.612– 625

Byström, P., Huss, M. and Persson, L., 2012. Ontogenetic constraints and diet shifts in Perch (*Perca fluviatilis*): mechanisms and consequences for intra-cohort cannibalism. *Freshwater Biology*, *57*(4), pp.847-857.

Charman, E.C., Smith, K.W., Dillon, I.A., Dodd, S., Gruar, D.J., Cristinacce, A., Grice, P.V. and Gregory, R.D., 2012. Drivers of low breeding success in the Lesser Spotted Woodpecker Dendrocopos minor in England: testing hypotheses for the decline. *Bird study*, *59*(3), pp.255-265.

Chess, K.F. and Ringo, J.M., 1985. Oviposition site selection by *Drosophila melanogaster* and *Drosophila simulans*. *Evolution*, *39*(4), pp.869-877.

Chevin, L.M., Lande, R. and Mace, G.M., 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS biology*, *8*(4), p.e1000357.

Chown, S.L. and Gaston, K.J., 2010. Body size variation in insects: a macroecological perspective. *Biological Reviews*, *85*(1), pp.139-169.

Claessen, D., De Roos, A.M. and Persson, L., 2004. Population dynamic theory of size–dependent cannibalism. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1537), pp.333-340.

Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., Maccoll, A.D.C., Kansky, R., Chadwick, P., Manser, M., Skinner, J.D. and Brotherton, P.N.M., 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *Journal of Animal Ecology*, *68*(4), pp.672-683.

Colchen, T., Fontaine, P., Ledoré, Y., Teletchea, F. and Pasquet, A., 2019. Intra-cohort cannibalism in early life stages of pikeperch. *Aquaculture Research*, *50*(3), pp.915-924.

Courchamp, F., Clutton-Brock, T. and Grenfell, B., 1999. Inverse density dependence and the Allee effect. *Trends in ecology & evolution*, *14*(10), pp.405-410.

Courchamp, F., Grenfell, B.T. and Clutton-Brock, T.H., 2000. Impact of natural enemies on obligately cooperative breeders. *Oikos*, *91*(2), pp.311-322.

Cote, J., Clobert, J., Brodin, T., Fogarty, S. and Sih, A., 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*(1560), pp.4065-4076.

Crook, J.R. and Shields, W.M., 1985. Sexually selected infanticide by adult male barn swallows. *Animal Behaviour*, *33*(3), pp.754-761.

Crump, M.L., 1983. Opportunistic cannibalism by amphibian larvae in temporary aquatic environments. *The American Naturalist*, *121*(2), pp.281-289.

Crump, M. L. 1992. Cannibalism in amphibians. Pages 256–276i n M. A. Elgar and B. J. Crespi, editors. Cannibalism: ecology and evolution in diverse taxa. Oxford University Press, Oxford, UK.

Cunha, F.C.R.D., Fontenelle, J.C.R. and Griesser, M., 2017. Predation risk drives the expression of mobbing across bird species. *Behavioral Ecology*, *28*(6), pp.1517-1523.

Dassow, C.J., Collier, A., Hodgson, J.Y., Buelo, C.D. and Hodgson, J.R., 2018. Filial cannibalism by largemouth bass (*Micropterus salmoides*): a three-decade natural history record from a small northern temperate lake. *Journal of Freshwater Ecology*, *33*(1), pp.361-379.

David, J.R., Gibert, P., Legout, H., Pétavy, G., Capy, P. and Moreteau, B., 2005. Isofemale lines in Drosophila: an empirical approach to quantitative trait analysis in natural populations. *Heredity*, *94*(1), p.3.

Dennis, B., 2002. Allee effects in stochastic populations. *Oikos*, *96*(3), pp.389-401.

DeAngelis, D.L. and Mooij, W.M., 2005. Individual-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution and Systematics*, *36*, pp.147-168.

Denno, R.F., 1994. The evolution of dispersal polymorphisms in insects: the influence of habitats, host plants and mates. *Population Ecology*, *36*(2), pp.127-135.

de Carvalho Guimarães, I., Cardoso, C.A.L., Lima, S.M., da Cunha Andrade, L.H. and Junior, W.F.A., 2016. Chemical signals might mediate interactions between females and juveniles of *Latrodectus geometricus* (Araneae: Theridiidae). *Behavioural processes*, *126*, pp.27-35.

Dingemanse, N.J., Wright, J., Kazem, A.J., Thomas, D.K., Hickling, R. and Dawnay, N., 2007. Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology*, *76*(6), pp.1128-1138.

Dobler, R. and Kölliker, M., 2009. Kin-selected siblicide and cannibalism in the European earwig. *Behavioral Ecology*, *21*(2), pp.257-263.

Dobson, A.P. and Lees, A.M., 1989. The population dynamics and conservation of primate populations. *Conservation Biology*, *3*(4), pp.362-380.

Driscoll, D.A. and Weir, T.O.M., 2005. Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. *Conservation Biology*, *19*(1), pp.182-194.

Duelli, P., 1981. Is larval cannibalism in lacewings adaptive? (Neuroptera: Chrysopidae). *Population Ecology*, *23*(2), pp.193-209.

Duffey, E., 1995. The distribution, status and habitats of *Dolomedes fimbriatus* (Clerck) and *D. plantarius* (Clerck) in Europe. *Proceedings of the 15th European Colloquium of Arachnology*, pp. 54 – 65.

Duffey, E., 2012. *Dolomedes plantarius* (Clerck, 1757)(Araneae: Pisauridae): a reassessment of its ecology and distribution in Europe, with comments on its history at Redgrave and Lopham Fen, England. *Arachnology*, *15*(8), pp.285-293.

Eastwood, L. and Burnet, B., 1977. Courtship latency in male *Drosophila melanogaster*. *Behavior genetics*, *7*(5), pp.359-372.

Elgar, M.A., 1991. Sexual cannibalism, size dimorphism, and courtship behavior in orb-weaving spiders (Araneidae). *Evolution*, *45*(2), pp.444-448.

Elgar, M. A. (1992). Sexual cannibalism in spiders and other invertebrates. In M. A. Elgar & B. J. Crespi (Eds.), Cannibalism: Ecology and evolution among diverse taxa (pp. 128– 155). Oxford: Oxford University Press.

Elgar, M.A. and Nash, D.R., 1988. Sexual cannibalism in the garden spider *Araneus diadematus*. *Animal Behaviour*, *36*(5), pp.1511-1517.

Elgar, M.A., Ghaffar, N. and Read, A.F., 1990. Sexual dimorphism in leg length among orb-weaving spiders: a possible role for sexual cannibalism. *Journal of Zoology*, *222*(3), pp.455-470.

Elgar, M.A. and Fahey, B.F., 1996. Sexual cannibalism, competition, and size dimorphism in the orb-weaving spider *Nephila plumipes* Latreille (Araneae: Araneoidea). *Behavioral Ecology*, *7*(2), pp.195-198.

Elgar, M. A., Schneider, J. M., & Herberstein, M. E., 2000. Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi*. *Proceedings of the Royal Society of London B: Biological Sciences*, *267*(1460), pp.2439– 2443

Fea, M.P., Stanley, M.C. and Holwell, G.I., 2014. Cannibalistic siblicide in praying mantis nymphs (*Miomantis caffra*). *Journal of ethology*, *32*(1), pp.43-51.

Fisher, A.M., Cornell, S.J., Holwell, G.I. and Price, T.A., 2018. Sexual cannibalism and population viability. *Ecology and evolution*, *8*(13), pp.6663-6670.

Folkvord, A., 1991. Growth, survival and cannibalism of cod juveniles (*Gadus morhua*): effects of feed type, starvation and fish size. *Aquaculture*, *97*(1), pp.41-59.

Forster, L. M., 1992. The stereotyped behavior of sexual cannibalism in *Latrodectus hasselti* Thorell (Araneae, Theridiidae), the Australian redback spider. *Australian Journal of Zoology*, *40*(1), pp.1– 11.

Fox, L.R., 1975. Cannibalism in natural populations. *Annual review of ecology and systematics*, *6*(1), pp.87-106.

Frankham, R., 1995. Effective population size/adult population size ratios in wildlife: a review. *Genetics Research*, *66*(2), pp.95-107.

Fromhage, L., Elgar, M.A. and Schneider, J.M., 2005. Faithful without care: the evolution of monogyny. *Evolution*, *59*(7), pp.1400-1405.

Fromhage, L., Jacobs, K. and Schneider, J.M., 2007. Monogynous mating behaviour and its ecological basis in the golden orb spider *Nephila fenestrata*. *Ethology*, *113*(8), pp.813-820.

Fromhage, L., McNamara, J.M. and Houston, A.I., 2008. A model for the evolutionary maintenance of monogyny in spiders. *Journal of Theoretical Biology*, *250*(3), pp.524-531.

Fromhage, L., & Schneider, J. M., 2006. Emasculation to plug up females: The significance of pedipalp damage in *Nephila fenestrata*. *Behavioral Ecology*, *17*(3), pp.353– 357.

Fromhage, L., Uhl, G., & Schneider, J. M., 2003. Fitness consequences of sexual cannibalism in female *Argiope bruennichi*. *Behavioral Ecology and Sociobiology*, *55*(1), pp.60– 64.

García-González, F., 2004. Infertile matings and sperm competition: the effect of "nonsperm representation" on intraspecific variation in sperm precedence patterns. *The American Naturalist*, *164*(4), pp.457-472.

Gardner, A., 2019. The greenbeard effect. *Current Biology*, *29*(11), pp.430-R431.

Gascoigne, J., Berec, L., Gregory, S. and Courchamp, F., 2009. Dangerously few liaisons: a review of mate-finding Allee effects. *Population Ecology*, *51*(3), pp.355-372.

Gaskett, A.C., 2007. Spider sex pheromones: emission, reception, structures, and functions. *Biological Reviews*, *82*(1), pp.27-48.

Gavín-Centol, M. P., Kralj-Fišer, S., De Mas, E., Ruiz-Lupión, D., & Moya-Laraño, J., 2017. Feeding regime, adult age and sexual size dimorphism as determinants of pre-copulatory sexual cannibalism in virgin wolf spiders. *Behavioral Ecology and Sociobiology*, *71*(1), 10.

Gemeno, C. and Claramunt, J., 2006. Sexual approach in the praying mantid *Mantis religiosa* (L.). *Journal of insect behavior*, *19*(6), pp.731-740.

Ghose, K., Triblehorn, J.D., Bohn, K., Yager, D.D. and Moss, C.F., 2009. Behavioral responses of big brown bats to dives by praying mantises. *Journal of Experimental Biology*, *212*(5), pp.693-703.

Gibson, J.S. and Uetz, G.W., 2008. Seismic communication and mate choice in wolf spiders: components of male seismic signals and mating success. *Animal Behaviour*, *75*(4), pp.1253-1262.

Giles, N., Wright, R.M. and Nord, M.E., 1986. Cannibalism in pike fry, *Esox lucius* L.: some experiments with fry densities. *Journal of Fish Biology*, *29*(1), pp.107-113.

Gray, S.M., Dill, L.M. and McKinnon, J.S., 2006. Cuckoldry incites cannibalism: male fish turn to cannibalism when perceived certainty of paternity decreases. *The American Naturalist*, *169*(2), pp.258-263.

Griffiths, S.W. and Magurran, A.E., 1999. Schooling decisions in guppies (*Poecilia reticulata*) are based on familiarity rather than kin recognition by phenotype matching. *Behavioral Ecology and Sociobiology*, *45*(6), pp.437-443.

Grimaldi, D. and Jaenike, J., 1984. Competition in natural populations of mycophagous *Drosophila*. *Ecology*, *65*(4), pp.1113-1120.

Grimm, V., 1999. Ten years of individual-based modelling in ecology: What have we learned and what could we learn in the future? *Ecological Modelling*, *115*(2), pp.129– 148.

Guttal, V., Romanczuk, P., Simpson, S.J., Sword, G.A. and Couzin, I.D., 2012. Cannibalism can drive the evolution of behavioural phase polyphenism in locusts. *Ecology letters*, *15*(10), pp.1158-1166.

Hamilton, W.D., 1964. The genetical evolution of social behaviour. II. *Journal of theoretical biology*, *7*(1), pp.17-52.

Hatchwell, B.J., Ross, D.J., Fowlie, M.K. and McGowan, A., 2001. Kin discrimination in cooperatively breeding long–tailed tits. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1470), pp.885-890.

Hassell, M. P., Lawton, J. H., & Beddington, J. R., 1976. The components of arthropod predation: I. The prey death-rate. *The Journal of Animal Ecology*, *45*(1), 135– 164.

Hebets, E. A., 2003. Subadult experience influences adult mate choice in an arthropod: Exposed female wolf spiders prefer males of a familiar phenotype. *Proceedings of the National Academy of Sciences*, *100*(23), pp.13390– 13395.

Hebets, E.A. and Uetz, G.W., 2000. Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae: Lycosidae). *Behavioral Ecology and Sociobiology*, *47*(4), pp.280-286.

Heinsohn, R.G., 1992. Cooperative enhancement of reproductive success in white-winged choughs. *Evolutionary Ecology*, *6*(2), pp.97-114.

Herberstein, M. E., Gaskett, A. C., Schneider, J. M., Vella, N. G. F., & Elgar, M. A., 2005. Limits to male copulation frequency: Sexual cannibalism and sterility in St Andrew's Cross spiders (Araneae, Araneidae). *Ethology*, *111*(11), pp.1050– 1061.

Herberstein, M., Schneider, J., & Elgar, M., 2002. Costs of courtship and mating in a sexually cannibalistic orb-web spider: Female mating strategies and their consequences for males. *Behavioral Ecology and Sociobiology*, *51*(5), pp.440– 446.

Hernández, L., Aisenberg, A. and Molina, J., 2018. Mating plugs and sexual cannibalism in the Colombian orb-web spider *Leucauge mariana*. *Ethology*, *124*(1), pp.1-13.

Hoare, J.M., Pledger, S., Nelson, N.J. and Daugherty, C.H., 2007. Avoiding aliens: behavioural plasticity in habitat use enables large, nocturnal geckos to survive Pacific rat invasions. *Biological Conservation*, *136*(4), pp.510-519.

Hoffman, E.A. and Pfennig, D.W., 1999. Proximate causes of cannibalistic polyphenism in larval tiger salamanders. *Ecology*, *80*(3), pp.1076-1080.

Hollis, B., Kawecki, T.J. and Keller, L., 2015. No evidence that within-group male relatedness reduces harm to females in *Drosophila*. *Ecology and evolution*, *5*(4), pp.979-983.

Holwell, G.I., Allen, P.J.D., Goudie, F., Duckett, P.E. and Painting, C.J., 2016. Male density influences mate searching speed and copulation duration in millipedes (Polydesmida: *Gigantowales chisholmi*). *Behavioral ecology and sociobiology*, *70*(8), pp.1381-1388.

Holwell, G.I., Barry, K.L. and Herberstein, M.E., 2007. Mate location, antennal morphology, and ecology in two praying mantids (Insecta: Mantodea). *Biological Journal of the Linnean Society*, *91*(2), pp.307-313.

Hopper, K.R., Crowley, P.H. and Kielman, D., 1996. Density dependence, hatching synchrony, and within-cohort cannibalism in young dragonfly larvae. *Ecology*, *77*(1), pp.191-200.

Huntingford, F.A., 1976. The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour*, *24*(2), pp.245-260.

Hurd, L. E., Eisenberg, R. M., Fagan, W. F., Tilmon, K. J., Snyder, W. E., Vandersall, K. S., Datz, S. G. and Welch, J. D., 1994. Cannibalism reverses male-biased sex ratio in adult mantids: Female strategy against food limitation? *Oikos*, *69*, pp.193– 198.

Ioannou, C.C., Guttal, V. and Couzin, I.D., 2012. Predatory fish select for coordinated collective motion in virtual prey. *Science*, *337*(6099), pp.1212-1215.

IUCN, 2012. IUCN Red List of Threatened Species. Version 2012.1. International Union for Conservation of Nature and Natural Resources, Cambridge.

Johnson, J.C., 2001. Sexual cannibalism in fishing spiders (*Dolomedes triton*): an evaluation of two explanations for female aggression towards potential mates. *Animal Behaviour*, *61*(5), pp.905-914.

Johnson, J.C., 2004. Cohabitation of juvenile females with mature males promotes sexual cannibalism in fishing spiders. *Behavioral Ecology*, *16*(1), pp.269-273.

Johnson, J. C., and Sih, A., 2005. Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): A role for behavioral syndromes. *Behavioral Ecology and Sociobiology*, *58*(4), pp.390– 396.

Johnson, J.C. and Sih, A., 2007. Fear, food, sex and parental care: a syndrome of boldness in the fishing spider, *Dolomedes triton*. *Animal Behaviour*, *74*(5), pp.1131-1138.

Johnson, J.C., Trubl, P., Blackmore, V. and Miles, L., 2011. Male black widows court well-fed females more than starved females: silken cues indicate sexual cannibalism risk. *Animal Behaviour*, *82*(2), pp.383-390.

Johnson, D.M., Liebhold, A.M., Tobin, P.C. and Bjørnstad, O.N., 2006. Allee effects and pulsed invasion by the gypsy moth. *Nature*, *444*(7117), p.361.

Kasumovic, M.M., Bruce, M.J., Herberstein, M.E. and Andrade, M.C., 2006. Risky mate search and mate preference in the golden orb-web spider (*Nephila plumipes*). *Behavioral Ecology*, *18*(1), pp.189-195.

Keller, L. and Ross, K.G., 1998. Selfish genes: a green beard in the red fire ant. *Nature*, *394*(6693), p.573.

Khwaja, N., Briskie, J.V. and Hatchwell, B.J., 2019. Individuality, kin similarity and experimental playback of contact calls in cooperatively breeding riflemen. *New Zealand Journal of Zoology*, pp.1-14.

Kindvall, O., Vessby, K., Berggren, Å. and Hartman, G., 1998. Individual mobility prevents an Allee effect in sparse populations of the bush cricket *Metrioptera roeseli*: an experimental study. *Oikos*, pp.449-457.

Kohlmeier, C. and Ebenhöh, W., 1995. The stabilizing role of cannibalism in a predator-prey system. *Bulletin of Mathematical Biology*, *57*(3), pp.401-411.

Kralj-Fišer, S., Čandek, K., Lokovšek, T., Čelik, T., Cheng, R. C., Elgar, M. A., & Kuntner, M., 2016. Mate choice and sexual size dimorphism, not personality, explain female aggression and sexual cannibalism in raft spiders. *Animal Behaviour*, *111*, pp. 49– 55.

Kuussaari, M., Saccheri, I., Camara, M. and Hanski, I., 1998. Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos*, *82*(2), pp.384-392.

Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist*, *142*(6), pp.911-927.

Langellotto, G.A., Denno, R.F. and Ott, J.R., 2000. A trade-off between flight capability and reproduction in males of a wing-dimorphic insect. *Ecology*, *81*(3), pp.865-875.

Lawrence, S.E., 1992. Sexual cannibalism in the praying mantid, *Mantis religiosa*: a field study. *Animal Behaviour*, *43*(4), pp.569-583.

Lehmann, G.U., 2007. Density-dependent plasticity of sequential mate choice in a bushcricket (Orthoptera: Tettigoniidae). *Australian Journal of Zoology*, *55*(2), pp.123-130.

Lelito, J. P., & Brown, W. D., 2006. Complicity or conflict over sexual cannibalism? Male risk taking in the praying mantis *Tenodera aridifolia sinensis*. *The American Naturalist*, *168*(2), pp.263–269.

Lelito, J.P. and Brown, W.D., 2008. Mate attraction by females in a sexually cannibalistic praying mantis. *Behavioral Ecology and Sociobiology*, *63*(2), pp.313-320.

Lennartsson, T., 2002. Extinction thresholds and disrupted plant–pollinator interactions in fragmented plant populations. *Ecology*, *83*(11), pp.3060-3072.

Leroy, B., Paschetta, M., Canard, A., Bakkenes, M., Isaia, M. and Ysnel, F., 2013. First assessment of effects of global change on threatened spiders: Potential impacts on *Dolomedes plantarius* (Clerck) and its conservation plans. *Biological Conservation*, *161*, pp.155-163.

Lihoreau, M., Zimmer, C. and Rivault, C., 2007. Kin recognition and incest avoidance in a group-living insect. *Behavioral Ecology*, *18*(5), pp.880-887.

Lizé, A., Carval, D., Cortesero, A.M., Fournet, S. and Poinsot, D., 2006. Kin discrimination and altruism in the larvae of a solitary insect. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1599), pp.2381-2386.

Loekle, D.M., Madison, D.M. and Christian, J.J., 1982. Time dependency and kin recognition of cannibalistic behavior among poeciliid fishes. *Behavioral and Neural Biology*, *35*(3), pp.315-318.

Manley, C.B., Rakocinski, C.F., Lee, P.G. and Blaylock, R.B., 2015. Feeding frequency mediates aggression and cannibalism in larval hatchery-reared spotted seatrout, *Cynoscion nebulosus*. *Aquaculture*, *437*, pp.155-160.

Marden, J.H., 1989. Bodybuilding dragonflies: costs and benefits of maximizing flight muscle. *Physiological Zoology*, *62*(2), pp.505-521.

Markman, S., Hill, N., Todrank, J., Heth, G. and Blaustein, L., 2009. Differential aggressiveness between fire salamander (*Salamandra infraimmaculata*) larvae covaries with their genetic similarity. *Behavioral ecology and sociobiology*, *63*(8), pp.1149-1155.

Maxwell, M. R., Gallego, K. M., & Barry, K. L., 2010. Effects of female feeding regime in a sexually cannibalistic mantid: Fecundity, cannibalism, and male response in *Stagmomantis limbata* (Mantodea). *Ecological Entomology*, *35*(6), pp.775– 787.

Mehlis, M., Bakker, T.C., Engqvist, L. and Frommen, J.G., 2010. To eat or not to eat: egg-based assessment of paternity triggers fine-tuned decisions about filial cannibalism. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1694), pp.2627-2635.

Michaud, J.P., 2003. A comparative study of larval cannibalism in three species of ladybird. *Ecological entomology*, *28*(1), pp.92-101.

Miller, K.A., Nelson, N. J., Smith, H.G. & Moore, J. A., 2009. How do reproductive skew and founder group size affect genetic diversity in reintroduced populations?. *Molecular ecology*, *18*(18), pp.3792– 3802.

Mitsui, H. and Kimura, M.T., 2000. Coexistence of drosophilid flies: aggregation, patch size diversity and parasitism. *Ecological Research*, *15*(1), pp.93-100.

Mole, S. and Zera, A.J., 1993. Differential allocation of resources underlies the dispersal-reproduction trade-off in the wing-dimorphic cricket, *Gryllus rubens*. *Oecologia*, *93*(1), pp.121-127.

Murphy, D.D., Launer, A.E. and Ehrlich, P.R., 1983. The role of adult feeding in egg production and population dynamics of the checkerspot butterfly *Euphydryas editha*. *Oecologia*, *56*(2-3), pp.257-263.

Møller, A.P. and Legendre, S., 2001. Allee effect, sexual selection and demographic stochasticity. *Oikos*, *92*(1), pp.27-34.

Narasimha, S., Nagornov, K.O., Menin, L., Mucciolo, A., Rohwedder, A., Humbel, B.M., Stevens, M., Thum, A.S., Tsybin, Y.O. and Vijendravarma, R.K., 2019. *Drosophila melanogaster* cloak their eggs with pheromones, which prevents cannibalism. *PLoS biology*, *17*(1), p.e2006012.

Newman, J. A., & Elgar, M. A., 1991. Sexual cannibalism in orb-weaving spiders: An economic model. *The American Naturalist*, *138*(6), pp.1372– 1395.

Nessler, S.H., Uhl, G. and Schneider, J.M., 2006. Genital damage in the orb-web spider *Argiope bruennichi* (Araneae: Araneidae) increases paternity success. *Behavioral Ecology*, *18*(1), pp.174-181.

Nummelin, M., 1989. Cannibalism in waterstriders (Heteroptera: Gerridae): is there kin recognition? *Oikos*, pp.87-90.

Odum, H.T. and Allee, W.C., 1954. A note on the stable point of populations showing both intraspecific cooperation and disoperation. *Ecology*, *35*(1), pp.95-97.

Packer, C., 2000. Infanticide is no fallacy. *American Anthropologist*, *102*(4), pp.829-831.

Packer, C. and Pusey, A.E., 1983. Adaptations of female lions to infanticide by incoming males. *The American Naturalist*, *121*(5), pp.716-728.

Pereira, L.S., Agostinho, A.A. and Winemiller, K.O., 2017. Revisiting cannibalism in fishes. *Reviews in Fish Biology and Fisheries*, *27*(3), pp.499-513.

Persson, L., Byström, P. and Wahlström, E., 2000. Cannibalism and competition in Eurasian perch: population dynamics of an ontogenetic omnivore. *Ecology*, *81*(4), pp.1058-1071.

Persons, M.H. and Uetz, G.W., 2005. Sexual cannibalism and mate choice decisions in wolf spiders: influence of male size and secondary sexual characters. *Animal Behaviour*, *69*(1), pp.83-94.

Petersen, A., Nielsen, K.T., Christensen, C.B. and Toft, S., 2010. The advantage of starving: success in cannibalistic encounters among wolf spiders. *Behavioral Ecology*, *21*(5), pp.1112-1117.

Petranka, J.W. and Thomas, D.A., 1995. Explosive breeding reduces egg and tadpole cannibalism in the wood frog, *Rana sylvatica*. *Animal Behaviour*, *50*(3), pp.731-739.

Pfennig, D., 1990. The adaptive significance of an environmentally-cued developmental switch in an anuran tadpole. *Oecologia*, *85*(1), pp.101-107.

Pfennig, D.W., 1999. Cannibalistic tadpoles that pose the greatest threat to kin are most likely to discriminate kin. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1414), pp.57-61.

Pfennig, D.W. and Collins, J.P., 1993. Kinship affects morphogenesis in cannibalistic salamanders. *Nature*, *362*(6423), p.836.

Pfennig, D.W., Sherman, P.W. and Collins, J.P., 1994. Kin recognition and cannibalism in polyphenic salamanders. *Behavioral Ecology*, *5*(2), pp.225-232.

Pfennig, D.W., Reeve, H.K. and Sherman, P.W., 1993. Kin recognition and cannibalism in spadefoot toad tadpoles. *Animal Behaviour*, *46*(1), pp.87-94.

Pizzatto, L. and Shine, R., 2008. The behavioral ecology of cannibalism in cane toads (*Bufo marinus*). *Behavioral Ecology and Sociobiology*, *63*(1), pp.123-133.

Polis, G.A., 1981. The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics*, *12*(1), pp.225-251.

Prenter, J., MacNeil, C. and Elwood, R.W., 2006. Sexual cannibalism and mate choice. *Animal Behaviour*, *71*(3), pp.481-490.

Pruitt, J. N., Berning, A. W., Cusack, B., Shearer, T. A., McGuirk, M., Coleman, A., Eng, R. Y. Y., Armagost, F., Sweeney, K. and Singh, N., 2014. Precopulatory sexual cannibalism causes increase egg case production, hatching success, and female attractiveness to males. *Ethology*, *120*(5), pp.453– 462.

Pruitt, J.N., Riechert, S.E. and Jones, T.C., 2008. Behavioural syndromes and their fitness consequences in a socially polymorphic spider, *Anelosimus studiosus*. *Animal Behaviour*, *76*(3), pp.871-879.

Queller, D.C., Ponte, E., Bozzaro, S. and Strassmann, J.E., 2003. Single-gene greenbeard effects in the social amoeba *Dictyostelium discoideum*. *Science*, *299*(5603), pp.105-106.

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

R Core Team. (2017). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/.

Rabaneda-Bueno, R., Rodríguez-Gironés, M.Á., Aguado-de-la-Paz, S., Fernández-Montraveta, C., De Mas, E., Wise, D.H. and Moya-Laraño, J., 2008. Sexual cannibalism: high incidence in a natural population with benefits to females. *PLoS One*, *3*(10), p.e3484.

Ramsay, G.W., 1990. Mantodea (Insecta), with a review of aspects of functional morphology and biology. *Fauna of New Zealand*, *19*.

Rhainds, M., 2019. Ecology of female mating failure/lifelong virginity: a review of causal mechanisms in insects and arachnids. *Entomologia Experimentalis et Applicata*, *167*(1), pp.73-84.

Rich, E.R. 1956. Egg cannibalism and fecundity in *Tribolium*. *Ecology, 37*(1), 109-120.

Ricker, W.E., 1954. Stock and recruitment. *Journal of the Fisheries Board of Canada*, *11*(5), pp.559-623.

Riechert, S.E. and Hedrick, A.V., 1993. A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta* (Araneae, Agelenidae). *Animal Behaviour*, *46*(4), pp.669-675.

Roberts, J.A. and Uetz, G.W., 2005. Information content of female chemical signals in the wolf spider, *Schizocosa ocreata*: male discrimination of reproductive state and receptivity. *Animal Behaviour*, *70*(1), pp.217-223.

Robertson, B.A., Rehage, J.S. and Sih, A., 2013. Ecological novelty and the emergence of evolutionary traps. *Trends in ecology & evolution*, *28*(9), pp.552-560.

Roggenbuck, H., Pekár, S., & Schneider, J. M., 2011. Sexual cannibalism in the European garden spider *Araneus diadematus*: The roles of female hunger and mate size dimorphism. *Animal Behaviour*, *81*(4), pp.749– 755.

Rohwer, S., 1986. Selection for adoption versus infanticide by replacement "mates" in birds. In *Current ornithology* (pp. 353-395). Springer, Boston, MA.

Rossmanith, E., Blaum, N., Höntsch, K. and Jeltsch, F., 2009. Sex-related parental care strategies in the lesser spotted woodpecker *Picoides minor*: of flexible mothers and dependable fathers. *Journal of Avian Biology*, *40*(1), pp.28-33.

Samu, F., Toft, S. and Kiss, B., 1999. Factors influencing cannibalism in the wolf spider *Pardosa agrestis* (Araneae, Lycosidae). *Behavioral Ecology and Sociobiology*, *45*(5), pp.349-354.

Schielzeth, H. and Nakagawa, S., 2011. rptR: Repeatability for Gaussian and non-Gaussian data. *R package*.

Schlaepfer, M.A., Runge, M.C. and Sherman, P.W., 2002. Ecological and evolutionary traps. *Trends in Ecology & Evolution*, *17*(10), pp.474-480.

Schmitz, O.J. and Suttle, K.B., 2001. Effects of top predator species on direct and indirect interactions in a food web. *Ecology*, *82*(7), pp.2072-2081.

Schneider, J.M. and Elgar, M.A., 2001. Sexual cannibalism and sperm competition in the golden orb-web spider *Nephila plumipes* (Araneoidea): female and male perspectives. *Behavioral Ecology*, *12*(5), pp.547-552.

Schneider, J.M. and Elgar, M.A., 2002. Sexual cannibalism in *Nephila plumipes* as a consequence of female life history strategies. *Journal of Evolutionary Biology*, *15*(1), pp.84-91.

Schneider, J. and Fromhage, L., 2010. Monogynous mating strategies in spiders. In *Animal behaviour: evolution and mechanisms*, pp. 441-464.

Schneider, J. M., & Lesmono, K., 2009. Courtship raises male fertilization success through post-mating sexual selection in a spider. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*(1670), pp.3105– 3111.

Schwartz, S.K., Wagner Jr, W.E. and Hebets, E.A., 2013. Spontaneous male death and monogyny in the dark fishing spider. *Biology letters*, *9*(4), p.20130113.

Schwartz, S.K., Wagner Jr, W.E. and Hebets, E.A., 2014. Obligate male death and sexual cannibalism in dark fishing spiders. *Animal behaviour*, *93*, pp.151-156.

Schwartz, S.K., Wagner Jr, W.E. and Hebets, E.A., 2016. Males can benefit from sexual cannibalism facilitated by self-sacrifice. *Current Biology*, *26*(20), pp.2794-2799.

Shaw, A.K. and Kokko, H., 2014. Mate finding, Allee effects and selection for sex-biased dispersal. *Journal of Animal Ecology*, *83*(6), pp.1256-1267.

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

Sih, A., Cote, J., Evans, M., Fogarty, S. and Pruitt, J., 2012. Ecological implications of behavioural syndromes. *Ecology letters*, *15*(3), pp.278-289.

Sih, A., Ferrari, M.C. and Harris, D.J., 2011. Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary applications*, *4*(2), pp.367-387.

Smith, H., 2000. The status and conservation of the fen raft spider (*Dolomedes plantarius*) at Redgrave and Lopham Fen National Nature Reserve, England. *Biological Conservation*, *95*(2), pp.153-164.

Smith, B.R. and Blumstein, D.T., 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, *19*(2), pp.448-455.

Smith, C. and Reay, P., 1991. Cannibalism in teleost fish. *Reviews in Fish Biology and Fisheries*, *1*(1), pp.41-64.

Sogard, S.M. and Olla, B.L., 1994. The potential for intracohort cannibalism in age-0 walleye pollock, *Theragra chalcogramma*, as determined under laboratory conditions. *Environmental Biology of Fishes*, *39*(2), pp.183-190.

Spence, J. R., Zimmermann, M., & Wojcicki, J. P., 1996. Effects of food limitation and sexual cannibalism on reproductive output of the nursery web spider *Dolomedes triton* (Araneae: Pisauridae). *Oikos*, *75*, pp.373– 382.

Stratton, G.E. and Uetz, G.W., 1983. Communication via substratum-coupled stridulation and reproductive isolation in wolf spiders (Araneae: Lycosidae). *Animal Behaviour*, *31*(1), pp.164-172.

Stephens, P.A. and Sutherland, W.J., 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology & Evolution*, *14*(10), pp.401-405.

Suter, R.B., 1999. Cheap transport for fishing spiders (Araneae, Pisauridae): the physics of sailing on the water surface. *Journal of Arachnology*, pp.489-496.

Takasu, F., 2009. Individual-based modelling of the spread of pine wilt disease: vector beetle dispersal and the Allee effect. *Population Ecology*, *51*(3), pp.399-409.

Tcheslavskaia, K., Brewster, C.C. and Sharov, A.A., 2002. Mating success of gypsy moth (Lepidoptera: Lymantriidae) females in southern Wisconsin. *The Great Lakes Entomologist*, *35*(1), p.1.

Tietjen, W.J., 1977. Dragline-following by male lycosid spiders. *Psyche: A Journal of Entomology*, *84*(2), pp.165-178.

Uetz, G.W., Papke, R. and Kilinc, B., 2002. Influence of feeding regime on body size, body condition and a male secondary sexual character in Schizocosa ocreata wolf spiders (Araneae, Lycosidae): condition-dependence in a visual signaling trait. *The Journal of Arachnology*, *30*(3), pp.461-470.

Valdés, E.S., Shelton, P.A., Armstrong, M.J. and Field, J.G., 1987. Cannibalism in South African anchovy: egg mortality and egg consumption rates. *South African Journal of Marine Science*, *5*(1), pp.613-622.

Vallon, M., Grom, C., Kalb, N., Sprenger, D., Anthes, N., Lindström, K. and Heubel, K.U., 2016. You eat what you are: personality-dependent filial cannibalism in a fish with paternal care. *Ecology and evolution*, *6*(5), pp.1340-1352.

Van Buskirk, J., 1989. Density-dependent cannibalism in larval dragonflies. *Ecology*, *70*(5), pp.1442-1449.

Veit, R.R. and Lewis, M.A., 1996. Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. *The American Naturalist*, *148*(2), pp.255-274.

Via, S., 1999. Cannibalism facilitates the use of a novel environment in the flour beetle, *Tribolium castaneum*. *Heredity*, *82*(3), p.267.

Vijendravarma, R.K., Narasimha, S. and Kawecki, T.J., 2013. Predatory cannibalism in *Drosophila melanogaster* larvae. *Nature communications*, *4*, p.1789.

Vugdelić, M., 2006. Genetic Relations Within and Among *Dolomedes* Aquatic Spiders. PhD Thesis, University of East Anglia, Norwich.

Walker, L.A. and Holwell, G.I., 2015. Sexual cannibalism in a facultative parthenogen: the springbok mantis (*Miomantis caffra*). *Behavioral Ecology*, *27*(3), pp.851-856.

Walls, S.C. and Roudebush, R.E., 1991. Reduced aggression toward siblings as evidence of kin recognition in cannibalistic salamanders. *The American Naturalist*, *138*(4), pp.1027-1038.

Ward, A.J. and Hart, P.J., 2003. The effects of kin and familiarity on interactions between fish. *Fish and Fisheries*, *4*(4), pp.348-358.

Watson, D.M., 2011. A productivity-based explanation for woodland bird declines: poorer soils yield less food. *Emu-Austral Ornithology*, *111*(1), pp.10-18.

Wells, H., Strauss, E.G., Rutter, M.A. and Wells, P.H., 1998. Mate location, population growth and species extinction. *Biological Conservation*, *86*(3), pp.317-324.

West-Eberhard, M.J., 1989. Phenotypic plasticity and the origins of diversity. *Annual review of Ecology and Systematics*, *20*(1), pp.249-278.

Wilder, S.M. and Rypstra, A.L., 2008. Sexual size dimorphism predicts the frequency of sexual cannibalism within and among species of spiders. *The American Naturalist*, *172*(3), pp.431-440.

Wilder, S.M., Rypstra, A.L. and Elgar, M.A., 2009. The importance of ecological and phylogenetic conditions for the occurrence and frequency of sexual cannibalism. *Annual Review of Ecology, Evolution, and Systematics*, *40*, pp.21-39.

Wildy, E.L., Chivers, D.P., Kiesecker, J.M. and Blaustein, A.R., 2001. The effects of food level and conspecific density on biting and cannibalism in larval long-toed salamanders, *Ambystoma macrodactylum*. *Oecologia*, *128*(2), pp.202-209.

Wilgers, D.J. and Hebets, E.A., 2012. Age-related female mating decisions are condition dependent in wolf spiders. *Behavioral Ecology and Sociobiology*, *66*(1), pp.29-38.

Wise, D.H., 1995. *Spiders in ecological webs*. Cambridge University Press.

Wittmer, H.U., Sinclair, A.R. and McLellan, B.N., 2005. The role of predation in the decline and extirpation of woodland caribou. *Oecologia*, *144*(2), pp.257-267.

Yamawaki, Y., 2003. Responses to worm-like-wriggling models by the praying mantis: effects of amount of motion on prey recognition. *Journal of ethology*, *21*(2), pp.123-129.

Yang, S., Yang, K., Liu, C., Sun, J., Zhang, F., Zhang, X. and Song, Z., 2015. To what extent is cannibalism genetically controlled in fish? A case study in juvenile hybrid catfish *Silurus meridionalis–asotus* and the progenitors. *Aquaculture*, *437*, pp.208-214.

Yasuda, H. and Ohnuma, N., 1999. Effect of cannibalism and predation on the larval performance of two ladybird beetles. *Entomologia experimentalis et applicata*, *93*(1), pp.63-67.

Zimmermann, M. and Spence, J.R., 1992. Adult population dynamics and reproductive effort of the fishing spider *Dolomedes triton* (Araneae, Pisauridae) in central Alberta. *Canadian Journal of Zoology*, *70*(11), pp.2224-2233.

Zimmer, S.M., Welke, K.W. and Schneider, J.M., 2012. Determinants of natural mating success in the cannibalistic orb-web spider *Argiope bruennichi*. *PloS one*, *7*(2), p.e31389.

Appendix 1: R code used to run the deterministic model used in Chapter 1

```
#----------------------------------------------------------------------
#XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
#----------------------------------------------------------------------
#A deterministic model of a sexually cannibalistic mating system
#R coding language
#----------------------------------------------------------------------
#XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
#----------------------------------------------------------------------


plotResolution <- 1001

#pre-copulatory cannibalism rate
c1 <- seq(0, 1, length = plotResolution)

c1Scale <- c1*100

#max number of matings
h <- 2

#number of new offspring created per mating in absence of cannibalism
a <- 1

#additional number of offspring that can be gained from cannibalism alone
b <- seq(0, 10, length = 5)

#empty matrix for collecting growth rate values
emptyMatrix <- matrix(0, nrow = length(b), ncol = length(c1))

for(i in 1:length(b)){
        for(j in 1:length(c1)){
                sumParts <- c()
                for(k in 1:(h-1)){
                        sumParts[k] <- ((1 - c1[j]) * (1 - c1[j]))^k
                        }
                sumTot <- sum(sumParts) #Sums number of matings after a maximum of h
mating opportunities
                r <- (1 - c1[j]) * (1 + sumTot) * (a + (b[i] * c1[j]) + (b[i] * c1[j]))
                emptyMatrix[i, j] <- r
        }
}

plot(c1Scale, emptyMatrix[5, ], type = "n", xlab = "cannibalism rate (%)", ylab = "population
growth rate", yaxt ='n', cex.lab = 1.25)
        lines(c1Scale, emptyMatrix[1, ], lwd = 2.5, lty = 2)
        lines(c1Scale, emptyMatrix[2, ], col = 'green', lwd = 2.5)
        lines(c1Scale, emptyMatrix[3, ], col = 'blue', lwd = 2.5)
        lines(c1Scale, emptyMatrix[4, ], col = 'red', lwd = 2.5)
        lines(c1Scale, emptyMatrix[5, ], lwd = 2.5)
        axis(side = 2, at = 1, las = 2)
        axis(side = 2, at = 0, las = 2)
        abline(h = 1, lty = 2)
        legend(80, 7.5, c(0, 2.5, 5, 7.5, 10), lty = c(2, 1, 1, 1, 1), lwd = c(2.5, 2.5, 2.5, 2.5,
2.5), col = c('black', 'green', 'blue', 'red', 'black'), bty = 'n', title = 'b=', cex = 0.75)
```

Appendix 2: R code used to run the stochastic model used Chapter 1

```
#------------------------------------------------------------------
#XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
#------------------------------------------------------------------
#A stochastic population simulation of a sexually cannibalistic mating system
#R coding language
#------------------------------------------------------------------
#XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
#------------------------------------------------------------------

#The function below defines the daily probabilities of a particular scenario happening to a male
#the function outputs the number of surviving males, the number of matings that have taken
#place and the number of receptive females left after 1 day

matingOutcomes <- function(carryingCap, malePopulation, receptiveFemales,
deathCannibalismPre, deathCannibalismPost, death){
        theta <- carryingCap * 0.01
        locate <- ((receptiveFemales/(receptiveFemales + theta))*2)/seasonLengthDays #Mate
finding prob has a type II response to the number of receptive females
        nothing <- 1 - (locate + death)
        naturalDeaths <- death
        locateMate <- locate *(1 - deathCannibalismPre)
        locateDie <- locate * deathCannibalismPre
        locateMateDie <- locateMate * deathCannibalismPost
        locateMateSurvive <- locateMate * (1 - deathCannibalismPost)
        possibleOutcomes <- c("NA","D", "LD", "LMD", "LMS")
        dailyOutcomes <- rmultinom(1, size = malePopulation,
                    prob = c(nothing, naturalDeaths, locateDie, locateMateDie,
locateMateSurvive))
        pNothing <- dailyOutcomes[1]
        pNaturalDeaths <- dailyOutcomes[2]
        pLocateDie <- dailyOutcomes[3]
        pLocateMateDie <- dailyOutcomes[4]
        pLocateMateSurvive <- dailyOutcomes[5]

        remainingMales <- malePopulation - (pNaturalDeaths + pLocateDie + pLocateMateDie)
        numMatings <- pLocateMateDie + pLocateMateSurvive
        receptiveFemales <- receptiveFemales - numMatings
        malePopulation <- remainingMales

        count <- c(malePopulation, numMatings, receptiveFemales)
        return(count)
}

initialCondRepeats <- 50
resolution <- 101
generations <- 2
seasonLengthDays <- 90
initialCond <- seq(0.05, 0.5, length = initialCondRepeats)
carryingCap <- 1000
death <- 0.01
numLines <- 5
baselineFecundity <- 2

b <- seq(0, 10, length = numLines)*2

c1 <- seq(0, 1, length = resolution)  #Range of cannibalism probabilities
c1Scale <- (c1 * 100)
```

```
populationMatrix <- matrix(0, nrow = initialCondRepeats , ncol = generations)

multiLineMatrix <- matrix(0, nrow = numLines, ncol = resolution)

for(e in 1:length(b)){   #Loops through multiple b values to create growth rate vectors for
plotting

        for(f in 1:length(c1)){   #Loops through multiple cannibalism probabilities to creat
growth rate vectors for plotting

        deathCannibalismPre <- c1[f]
        deathCannibalismPost <- c1[f]

                for(h in 1:initialCondRepeats){        #Loops through a range of initial densities
to give an average growth rate for each c1 and b parameter value
                        Nt <- rep(0, length = generations)

                        malePopulation <- round(carryingCap*initialCond[h])
                        receptiveFemales <- round(carryingCap*initialCond[h])

                        newAdults <- malePopulation + receptiveFemales

                        Nt[1] <- newAdults

                        for(i in 2:generations){

                                maleCount <- c()
                                maleCount[1] <- malePopulation

                                femaleCount <- c()
                                femaleCount[1] <- receptiveFemales

                                matingCount <- c()
                                matingCount[1] <- 0

                                        for(j in 2:seasonLengthDays) {  #The function is run
for a number of days - intends to simulate a breeding season
                                                funcOutcomes <-
matingOutcomes(carryingCap, malePopulation, receptiveFemales, deathCannibalismPre,
deathCannibalismPost, death)
                                                malePopulation <- funcOutcomes[1]
                                                mating <- funcOutcomes[2]
                                                receptiveFemales <- rbinom(1, size =
funcOutcomes[3], prob = c(1-death, death))

                                                if(j > 42){
                                                        #After 42 days, females that have
already mated become receptive once again
                                                        receptiveFemales <- rbinom(1, size
= funcOutcomes[3], prob = c(1-death, death)) + rbinom(1, size = matingCount[j - 42], prob =
c(1-death, death))
                                                }
                                                femaleCount[j] <- receptiveFemales
                                                maleCount[j] <- malePopulation
                                                matingCount[j] <- mating
                                        }
                                sumMatings <- sum(matingCount[2:seasonLengthDays])
                                fecundity <- baselineFecundity + c1[f]*b[e] + c1[f]*b[e]
                                newAdults <- sum(rpois(sumMatings, fecundity))
```

```
                                        Nt[i] <- newAdults
                                        malePopulation <- newAdults/2
                                        receptiveFemales <- newAdults/2
                                }
                                populationMatrix[h, ] <- Nt
                        }
                        r <- c()
                        for(m in 1:length(populationMatrix[ , 1])){
                                r[m] <- populationMatrix[m, 2]/populationMatrix[m, 1]
                        }
                        growthRate <- mean(r)  #Takes mean growth rate over range of initial
conditions
                        multiLineMatrix[e, f] <- growthRate
                }
print(e)
}

plot(c1Scale, multiLineMatrix[5, ], type = "n", xlab = "cannibalism rate (%)", yaxt = 'n', ylab =
"population growth rate", ylim = c(0, max(multiLineMatrix)), cex.lab = 1.25)
        lines(c1Scale, multiLineMatrix[1, ], lty = 2, lwd = 2.5)
        lines(c1Scale, multiLineMatrix[2, ], lwd = 2.5, col = 'green')
        lines(c1Scale, multiLineMatrix[3, ], lwd = 2.5, col ='blue')
        lines(c1Scale, multiLineMatrix[4, ], lwd = 2.5, col = 'red')
        lines(c1Scale, multiLineMatrix[5, ], lwd = 2.5)
        axis(side = 2, at = 1, las = 2)
        axis(side = 2, at = 0, las = 2)
        abline(h = 1, lty = 2)
        legend(80, 4.1, c(0, 2.5, 5, 7.5, 10), lty = c(2, 1, 1, 1, 1), lwd = c(2.5, 2.5, 2.5, 2.5,
2.5), col = c('black', 'green', 'blue', 'red', 'black'), bty = 'n', title = 'b=', cex = 0.75)
```

Appendix 3: The R function used to run the individual-based model from Chapter 2

```
#-------------------------------------------------------------------------
#XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
#-------------------------------------------------------------------------
# An individual-based model inspired by sexual cannibalism

# The function is written in R coding language and simulates a sexually
# cannibalistic breeding season. The status of each female is tracked
# using a matrix where each column represents a specific female and
# each row represents one day. The function returns: 1) the number of
# matings that were not preceeded or followed immediately by cannibalism,
# 2) the number of matings that followed an instance of pre-copulatory
# cannibalism, and 3) the number of instances of post-copulatory
# cannibalism.
#-------------------------------------------------------------------------
#XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX
#-------------------------------------------------------------------------


aSeason <- function(males, females, seasonLength, c1, c2, theta, death){

        if(females == 0){
                return(c(0,0,0))
        }

        femaleMatrix <- matrix(NA, nrow=seasonLength, ncol=females)

        for(j in 1:seasonLength){
                males <- rbinom(1,males, prob=c(1-death, death))

                for(i in sample(1:ncol(femaleMatrix))){
                        if(males == 0){
                                break
                        }
                        locate <- males/(males + theta)*2/seasonLength
                        if(j<=42){
                                if("D"%in%femaleMatrix[,i]){
                                        next
                                }else if("c2"%in%femaleMatrix[,i]||"M"%in%femaleMatrix[,i]){
                                        next
                                }else if(rbinom(1,1, prob=c(death, 1-death))==1){
                                        femaleMatrix[j, i] <- 'D'
                                }else if(rbinom(1,1, prob=c(locate, 1-locate))==0){
                                        femaleMatrix[j, i] <- 'N'
                                }else if(rbinom(1,1, prob=c(c1, 1-c1))==1){
                                        femaleMatrix[j, i] <- 'c1'
                                        males <- males-1
                                }else if(rbinom(1,1, prob=c2)==1){
                                        femaleMatrix[j, i] <- 'c2'
                                        males <- males-1
                                }else{
                                        femaleMatrix[j, i] <- 'M'
                                }
                        }else if(j>42){
                                pregnancy <- j-42
                                if("D"%in%femaleMatrix[,i]){
```

```
                                    next
                            }else if('c2' %in% femaleMatrix[,i][pregnancy:j-1]||'M' %in%
                            femaleMatrix[,i][pregnancy:j-1]){
                                    next
                            }else if(rbinom(1,1, prob=c(death, 1-death))==1){
                                    femaleMatrix[j, i] <- 'D'
                            }else if(rbinom(1,1, prob=c(locate, 1-locate))==0){
                                    femaleMatrix[j, i] <- 'N'
                            }else if(rbinom(1,1, prob=c(c1, 1-c1))==1){
                                    femaleMatrix[j, i] <- 'c1'
                                    males <- males-1
                            }else if(rbinom(1,1, prob=c2)==1){
                                    femaleMatrix[j, i] <- 'c2'
                                    males <- males-1
                            }else{
                                    femaleMatrix[j, i] <- 'M'
                            }
                    }
            }
    }

    c1Matings <- 0
    matings <- 0
    c2Matings <- 0

    for(i in 1:length(femaleMatrix[1,])){
            eventsVec <- na.omit(femaleMatrix[,i])
            eventsVec <- eventsVec[eventsVec!='N']
            eventsVec <- eventsVec[eventsVec!='D']
            for(j in 1:length(eventsVec)){
                    if(length(eventsVec)==0){
                            break
                    }else if(eventsVec[j]=='c2'){
                            c2Matings <- c2Matings+1
                            next
                    }else if(eventsVec[j]=='M' && j>1 && eventsVec[j-1]=='c1'){
                            c1Matings <- c1Matings+1
                            next
                    }else if(eventsVec[j]=='M'){
                            matings <- matings+1
                    }
            }
    }
    matingOutcomes <- c(matings, c1Matings, c2Matings)

return(matingOutcomes)
}
```