**Title: Density-dependent aggression, courtship and sex ratio in a fishing spider**

**Running title: Reproductive behaviour in *D. fimbriatus***

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**Abstract**

Sexual cannibalism is common in spiders and can be advantageous for female fitness by increasing egg production. However, it is possible that under low mate density, females may be at risk of consuming all of the males they encounter prior to copulation. Cannibalistic females may be able to mitigate the risk of virgin death if they reduce cannibalism rates in response to low mate availability. Here, we attempted to manipulate perceived mate density and observe whether it affected female aggression towards males in the fen raft spider (*Dolomedes fimbriatus*). We predicted that female attack rate would increase in response to an increasing number of male encounters. 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. Some of the virgin females laid and guarded unfertilised egg cases, this made them unattractive to males, potentially reducing their reproductive lifespan prematurely.

**Keywords:** aggression, arachnid, courtship, mate encounter, sex ratio, sexual cannibalism, spider

**Introduction**

Behavioural plasticity, the ability of organisms to modify their behaviour to suit the environment, can be vital for sustaining individual fitness in a changing habitat (Chevin et al., 2010). The effects of plasticity on individual fitness have also been shown to scale up to the population-level and play a crucial role in predicting 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 result 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 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., unpublished data).

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 manipulated mate encounter rate 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. Male courtship effort is often thought to signal male quality in some cannibalistic spiders (Shamble et al., 2009). It has previously been shown that high courtship effort reduces 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*

We 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. We visited the reserve a total of 10 times over two years (2016 and 2017) between the months of April and June. On each visit we 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 are 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 22oC 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. We 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 mate encounter rate, we 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, we 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 time2. Time was included as a quadratic term to test for the presence of a non-linear relationship between the abundance of males and females 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 the male’s first and second encounter with a female 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 field surveys, 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 time2 (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 (Fromhage et al., 2007; Fromhage et al., 2008) 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 reason for these comparatively low attack rates could be 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). Similarly, there is evidence that high levels of male-male competition may also be enough to facilitate the persistence of monogyny in natural populations (Fromhage et al., 2008). 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 could be indicative of a system where males are unlikely to re-mate. 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*.

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