Chapter 9

Sexual Cannibalism: Why would you eat the (Potential) Father of your Children?

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Introduction

Sexual cannibalism, which can occur precopulatory (before sex), pericopulatory (during sex), and postcopulatory (after sex), refers to the act of a female consuming the courting male. The act itself is rare and occurs almost exclusively in arthropods such as spiders, scorpions, and mantids, with most orders of arachnids demonstrating sexual cannibalism (Newman & Elgar, 1991). Within each case there is a lot of variation on the benefits and consequences of sexual cannibalism and because of this there has been much debate between amongst biologists as to whether it is an evolutionarily adaptive behavior or not, and why it persists in nature if it isn't adaptive for either sex.

It's important to keep in mind some of the concepts that are incorporated into hypotheses that I will be studying in this chapter. Intersexual conflict is the idea that there are differing levels of parental investment between a mother and a father, and that those differing levels will manifest themselves in mating habits and child rearing. Intersexual conflict is seen within the adaptive foraging hypothesis as well as the aggressive spillover hypothesis and is an important concept to keep in mind when analyzing these ideas, especially since it is seen widely in arachnids (Schneider & Lubin, 1998). Another idea to keep in mind is nuptial gifts, which are essentially gifts to ensure that the female is either fed or 'happy' with a male so he may mate with her. The gift can lead to a successful mating and even a potentially healthier female if the gift is edible and high quality. Nuptial gifts are seen in a wide array of insects, including spiders and mantids. Some even propose that these gifts, at least in arachnids, are direct byproducts of intersexual conflicts like sexual cannibalism (Stålhandske, 2002).

There are a few hypotheses that have formed around sexual cannibalism, each with compelling studies and evidence supporting them. One hypothesis is the adaptive foraging hypothesis, which claims sexual cannibalism as a method to gather nutrients that have a great effect on fecundity for a female (Katherine L. Barry, Holwell, & Herberstein, 2008; Blamires, 2011; Newman & Elgar, 1991; Winkler & Hall, 2013). Another hypothesis is the Aggressive Spillover hypothesis, which attributes sexual cannibalism to excess veracity in females, making

it non-adaptive in mating (Arnqvist & Henriksson, 1997; Johnson, 2001; Morse, 2004). There is also the mate choice hypothesis, which essentially claims sexual cannibalism to be a method of mate choice in which an assessment of mate quality is performed and if a male isn't of high enough quality he is cannibalized (Persons & Uetz, 2005; Prenter, MacNeil, & Elwood, 2006; Wilder & Rypstra, 2008).

While research has led to the development of three major hypotheses for sexual cannibalism that are supported by empirical evidence, the studies only look at one particular species and it's likely that their hypothesis doesn't fit a different species in the same way. This high level of variation in sexual cannibalism between organisms shows that it is both adaptive and non-adaptive depending on the organism. This in combination with the overall phylogenetic spread of the sexual cannibalism points to the trait evolving convergently and manifesting itself differently in separate species and orders. It may be impossible to formulate a one-size fits all hypothesis for organisms displaying sexual cannibalism, but rather an organism and close relative specific set of hypotheses may be required to fully understand why sexual cannibalism persists.

Is Sexual Cannibalism Adaptive?

What is the adaptive foraging Hypothesis? – You look tasty and I need healthy kids, so good luck.

The adaptive foraging hypothesis is essentially the idea that sexual cannibalism is a method for a female to increase her fecundity by consuming her mate if she hasn't had enough food to ensure a good health status for herself. Rather than spending energy hunting for prey, she can simply cannibalize small males who attempt (and sometimes successfully) mate with her. This though is not adaptive for males, as they benefit less (if at all) with this mating strategy, highlighting a large intersexual conflict. There have been numerous studies on this hypothesis, most looking primarily at orb-weaving spiders and their mating habits.

A 1991 by Newman and Elgar is a key study behind the adaptive foraging hypothesis that studied orb-weaving spiders (*Araneus diadematus*) who present a precopulatory/pericopulatory sexual cannibalism system. The study proposes an economic model based on fecundity indicators such as mass and egg output, as well as male size – and predicts that if a female has been starved, she will see an increase in body mass by consuming a vulnerable male (Newman & Elgar, 1991). They focus on the link between foraging to body size, and interpret larger body size as a gauge of how good a mate a male/female may be, implying size recognition and assessment (Newman & Elgar, 1991). This also relies on the concept that foraging abilities are heritable, which is a large variable they do not attempt to prove. Foraging abilities would have to be heritable because for this foraging ability to be so wide spread and persistent in the orb-weaver it would have to be a natural instinct to cannibalize. Assumptions aside, the economic model itself is sound. Female reproductive output depends upon male pedipalp insertions and her body size, whereas male body size is the only major economic factor involved his reproductive success. If a female has been starved and cannibalizes a male before he may mate, she later produces higher quality eggs (due to her larger body size) than starved females who do not cannibalize (Newman & Elgar, 1991). Smaller males are in turn cannibalized more often than larger males, potentially ensuring higher quality male mates and higher quality eggs (Newman &

Elgar, 1991). This supports their claim that there is some level of mate recognition and a 'decision' is made to either allow the male to mate or to cannibalize him. In cannibalizing the male, the females increases their fecundity through higher offspring quality rather than through an immediate mating, which is in turn an adaptive trait for both females and males. This model, in the sense of economic-based systems, has been supported in other studies since then (Andrade, 1998; J. Chadwick Johnson, Trubl, Blackmore, & Miles, 2011).

A study by Blamires looks further at the effects of sexual cannibalism in orb-weavers, focusing primarily on the actual effects of the 'diet' on female fecundity. The study found that there was a possible increase in female fecundity via an increase in egg energy density, but the consumed male cannot provide any sort of investment for the eggs themselves (Blamires, 2011). Due to the nature of energy exchange, the female doesn't directly apply the energy acquired from food to the production of her eggs (Blamires, 2011). Rather, female body size directly allows the female to increase her egg density, which in turn increases the fecundity of the female. While the consumption of a male may only directly affect future fecundity during female adolescence, the female still gains energy and physical benefit from the consumption of a male, especially if that male is a high energy one (Blamires, 2011). The issue with this though is that smaller males are the ones more likely to be cannibalized, and will likely not fit the profile of a high energy meal, which is a potential problem with his model (G Arnqvist & Henriksson, 1997; Newman & Elgar, 1991). Blamires' study doesn't undermine the economic model that Newman & Elgar setup twenty years prior, but rather fine tunes the hypothesis by analyzing if the male actually experiences a fecundity increase and how much the female's fecundity increases from the consumption of a male suitor. Rather than being adaptive and beneficial for both sexes, the adaptive foraging hypothesis is more of a temporary health boost for females so that she may be better capable to ensure her survival and her offspring's survival. The lower-quality male she consumes has no bearing on her offspring's quality outside of her ability to survive and bear them. Sexual cannibalism is still beneficial to the female and as such an adaptive behavior.

Research on the Western Black Widow found a similar foraging based courtship system for a species that cannibalizes postcopulation, which is quite a bit different than what is seen in the orb weaver and more towards what is seen in mantids. The study found that males court well-fed (and as such, better foragers) females more often than starved females (J. Chadwick Johnson et al., 2011). The model is not exactly like the model proposed by Newman and Elgar, but supports that a female may have a tendency to cannibalize based upon her food-intake (J. Chadwick Johnson et al., 2011). Females that have had a steady flow of food are in better health, a state that is represented through web development and silk quality. The better a web and the higher tactile quality the silk the more resources a female has available to put into her web (J. Chadwick Johnson et al., 2011). Johnson's data suggests that males have adapted over time to avoid being cannibalized, highlighting that it isn't beneficial to males, as highlighted with the Blamires study. The behavior remains adaptive for the female though, as a high energy food can help increase her resource pool and increase silk quality. While it depends on a male still mating with a starved female, a female can increase her fecundity be cannibalizing a male. Since cannibalism occurs post-copulation, the females gain energy to help ensure her own survival. She also gains energy to help ensure a higher quality web for future matings if the male's insertion was unsuccessful. This further shows that the adaptive foraging hypothesis for sexual cannibalism is exactly as the name applies, adaptive.

There is a fair amount of evidence to support this hypothesis, especially in its fine tuned form that has come about with more research that doesn't assume some form of male benefit. While it's not impossible for a male to benefit from sexual cannibalism, he would have to have successfully mated and directly impacted the female's survival after copulation. The female though is the primary and clear benefactor of sexual cannibalism, particularly females that have been resource starved and need energy to ensure her own survival as well as the birth of her offspring. Adapting the way that she consumes energy to focus on high energy targets, males, is an easy way to do this as males come to her in a vulnerable position.

One may have noticed that all of these studies so far have focused on spiders – that's because of the rarity of sexual cannibalism. In the Arachnida class sexual cannibalism is seen in various, diverse families and species, as present in Figure 1. It is seen in the Insecta class as well though, and is often more famously acknowledged than sexual cannibalism in its arachnid relatives. This section of the chapter will examine organisms other than spiders that exhibit sexual cannibalism, including the somewhat closely related scorpions of the Arachnida class and the distantly related mantids of the Insecta class.

Mantids – The Ultimate Paternal Sacrifice

Looking at mantids, a 1988 study of fecundity in *Hierodula membranacea* by Birkhead *et al.* found that there was a correlation in female ootheca mass and the amount of food they had taken in. The larger the ootheca mass and density, the more offspring produced (Young, Lee, & Birkhead, 1988). The ootheca is a large protective sac that contains many eggs. Female were starved were more likely to cannibalize males, and those who did had and increased ootheca mass (Young et al., 1988). This not only supports the adaptive foraging hypothesis, but it also serves as the basis for the Barry *et al.* study that will be mentioned shortly in this section. It provides in-depth evidence of the direct fecundity increase in adult mantids through the consumption of food, something that has not been seen in spiders.

As said, this evidence gave rise to the research of Barry *et al.* which suggests that female praying mantids, *Pseudomantis albofimriata*, fits the adaptive foraging hypothesis constructed around Newman & Elgar's research on the orb weaver spider. They found that female mantids that cannibalized their male mates showed significantly increased body condition and egg mass (K. L. Barry, Holwell, & Herberstein, 2008). This highlights a direct fecundity increase that appears to be linked to the consumption of a higher energy male. These male mantids is quite a bit higher energy allometrically compared to what one would have seen in the spider studies as mantids are still sexually dimorphic, but males are closer to females in terms of size. They also found that females were more likely to cannibalize the male if they were hungry/in poor physical condition (K. L. Barry et al., 2008), which only further indicates that a female is adapting their foraging habits to maximize their health and offspring success. The males in this situation also benefit from sexual cannibalism as there are significantly radical health improvements for the female upon consuming a male. Since the cannibalism occurs post-copulation, the male's sacrifice of himself is like the ultimate nuptial gift for the female, ensuring that she and his future offspring survive. This is one situation where the male's sacrifice sees direct fecundity increase

through the act. This means that not only do mantids fit the adaptive foraging hypothesis's economic model, it's also adaptive in both sexes which we have yet to see in spiders.

More evidence of the adaptive foraging hypothesis can be seen in the species *Mantis religiosa*, as shown in a study by Lawrence. The study itself doesn't focus on female fecundity or male benefit in the species, but rather male behavior all together. They found that during the breeding seasons males avoided any sort of precopulatory mating signals to females (Lawrence, 1992). Those males who did attempt to mate focused their efforts on heavier females, well fed females (Lawrence, 1992). While this could very well be a situation of mate choice, as in females who are heavier would be better mates, it's likely more an adaption to allow the male to copulate multiple times without being cannibalized. Males would likely select a female that is less likely to cannibalize, and if a female is heavier that means she doesn't need to consume the male to ensure her health. This supports that she is adapting the way she is foraging for food dynamically, and uses sexual cannibalism to do so (Lawrence, 1992).

The studies mentioned in this subsection show that mantids still show sexual dimorphism, but the males are substantially closer to female size, whereas most male spiders in previous studies were substantially smaller than females in terms of body mass. This size difference allows males to provide more energy rich food to females who cannibalize them, and show a model in which the adaptive foraging hypothesis is supported clearly through statistical data and traceable increases in fecundity. (K. L. Barry et al., 2008; Young et al., 1988). While not mantis related, it's important to link these distant relatives back to the Arachnida class. These findings are backed up by Wilder and Rypstra (Wilder & Rypstra, 2008). Though not a direct link between food and fecundity, the study finds that sexual dimorphism plays a large role in sexual cannibalism frequency. The larger the dimorphic gap the more likely the female spider is to cannibalize male (Wilder & Rypstra, 2008). While Mantids are less dimorphic than spiders, their dimorphism still plays a role in their cannibalistic habits. If spiders were to have smaller dimorphic gaps, more may fit into the adaptive foraging hypothesis. Mantids remain novel though, primarily due to the direct food-fecundity link.

Scorpions – They're a quite a bit more closely related right?

Mantids certainly bring interesting information to light about sexual selection in terms of organism that are distantly related to spiders, but there are other Arachnids that are a bit more closely related to spiders that can provide information right? Scorpions are often referenced in academic conversations as demonstrating sexual cannibalisms, but the issue is that sexual cannibalism is rare in scorpions and the research on the group is sparse at best.

Peretti *et al.* looks at this lack of research specifically by providing synthesis of what has been examined (Peretti, Acosta, & Benton, 1999). The paper examines the research performed on 3 different scorpion species that have been shown to sexually cannibalize. None of the known species have been shown to cannibalize have been show to cannibalize post-copulation, so they fall in-line with the orb-weaver relatives in that aspect (Lawrence, 1992). In the species they studied, even a species known to cannibalize was shown that cannibalization of the male was rare. They only saw two cases of sexual cannibalism by starved females (Lawrence, 1992). This makes it hard to make a hypothesis as to why the scorpions cannibalize in general, if it's adaptive

or non-adaptive. They do suggest however, that given the evidence they have found, the scorpion species studied likely fit into an economic model of benefit, much like the adaptive foraging hypothesis (Lawrence, 1992). This would imply that scorpions also exhibit an adaptive form of sexual cannibalism where at least the female benefits in terms of fecundity to some level.

Sadly there is not a whole lot of research in the way of scorpions, outside of this study little has been done to hypothesize why scorpions exhibit sexual cannibalism, certainly not to level seen in mantids and spiders. There is bound to be valuable information from different scorpion species and how they mate. But, none the less there is information indicating that close and distant relatives all display sexual cannibalism as a mating habit, one that has persisted through evolution. These two relatives seem to fall more in line with the orb-weaver spiders, though each seems to have their own twist on things.

What is the mate choice Hypothesis? – You'll never be good enough for me, but he will.

The mate choice hypothesis is similar to the adaptive foraging hypothesis in that it also posits sexual cannibalism to be adaptive. A female uses sexual cannibalism not so much as an increase in energy but rather as a way to forcefully select who they do and do not mate with. If a male isn't up to the female's standards, she can cannibalize and ensure that the male cannot successfully mate with her at all, while allowing larger males to mate, but this is of course limited to sexually dimorphic species.

A 2006 study by Prenter *et al.* was a relatively early look at the mate choice hypothesis and claimed that mate choice had no empirical evidence to back it and was likely a misinterpretation of the adaptive foraging hypothesis (Prenter et al., 2006). While studies have found that females definitely cannibalize the males if they have been starved, there had been little investigation into the mechanism of choice and how males in sexually dimorphic species play a role in female choice (Prenter et al., 2006). While this study raises valid concerns and speaks against this hypothesis entirely, I've included it because it's a primary example of the back and forth arguments centered on sexual cannibalism. The study dismisses previous ideas based on observations of habits and instead attempts to attribute the observations to other hypotheses that study species that are known to fit those hypotheses, like the orb-weaver and the adaptive foraging Hypothesis (Prenter et al., 2006). Essentially, mate choice is a misinterpretation, and the fact that smaller male is cannibalized more often than a large male is simply matter of vulnerability as a meal rather than the female actively choosing the male for his fitness level (Prenter et al., 2006).

If Prenter's study were to be taken to heart and the mate choice hypothesis looked at objectively and regarded as false then valuable information would be lost. A 2011 study by Kralj-Fišer *et al.* looks at a nephilid spider (*Nephilengys livida*), which is sexually dimorphic like the orb-weavers seen in previous studies, but a different family for spider all together. Sexual cannibalism also occurs for the species during precopulatory and postcopulatory phases, which is quite a bit different than the orb-weavers' habits (Kralj-Fišer et al., 2011). They look at the nephilid spider under the lens of the mate choice hypothesis, rather than the adaptive foraging hypothesis. The study looked directly at the male relationship with sexual selection, examining exactly what types of males were more likely to be cannibalized. The study found that less

aggressive males were more likely to be preyed upon by any type of female, aggressive or non-aggressive (Kralj-Fišer et al., 2011). They looked at attempts to attack and cannibalize rather than overall success, so there was some level of decision made by the female. This supports the hypothesis that female can use sexual cannibalism to select for a higher quality male under the assumption that aggression equates to quality, which is the exact opposite of what Prenter claimed and more in line with the original mate choice hypothesis. This sort of choice system would provide benefits for the female, making sexual selection under this lens adaptive as well. This study though doesn't look into the impacts of health, which was one of the focuses of the adaptive foraging studies, and while it shows clear evidence for sexual selection through mate choice, it could be strengthened or weakened with how an economic model applies to the species. The study is also directly aimed as a response at the aggressive spillover hypothesis that I will be discussing shortly in the chapter. The authors use the study to state that aggressive spillover isn't the proper hypothesis for sexual cannibalism because it is a more calculated action than something mindless (Kralj-Fišer et al., 2011).

Though the evidence varies, and further research can clearly reveal new details, there's a large amount of research behind hypotheses that support a model of sexual selection that is directly beneficial to female fecundity. These energy benefits and mate choice are not mutually exclusive though, so the mate choice hypothesis certainly doesn't account for the whole picture. The controversy though is clear, as many studies have been conducted to disprove other hypotheses and many have heavily questioned the entire premise of other's research assumptions. In the next section of the chapter I'll be exploring the hypothesis that looks at sexual cannibalism as a non-adaptive system.

But could it be Non-Adaptive?

What is the aggressive spillover Hypothesis? – I'm going to eat you just because I feel like killing

The aggressive spillover hypothesis is often used to argue against the adaptive-foraging model, and looks at sexual cannibalism as more of a miscommunication of signals. Early studies suggest that other species of spiders, such as the fishing spider don't entirely support the whole adaptive foraging hypothesis (Arnqvist, 1992; Johnson, 2001). The hypothesis posits that sexual cannibalism is a remnant of female voracity from adolescence, in which the more aggressive a female was towards prey and predators, the more likely she was to survive and flourish. The habits simply stick from the developmental stage and 'spillover' into the adult stage. The name of the hypothesis is a bit of a misnomer, it should rather be called Voracity Spillover, but for the sake of its popular use I've elected to keep the name it is so frequently called.

A study by Henriksson and Arnqvist looks directly at the foraging model proposed by Newman and Elgar's 1991 study. Henriksson partnered with Arnqvist to expand on Arnqvist's original proposal of the aggressive spillover hypothesis (Goran Arnqvist, 1992). Henriksson examined the assumptions made and the expected outcomes of Newman & Elgar if their model should hold true for the sexually cannibalistic raft spider. The study concluded that the adaptive-foraging model that Newman and Elgar presented for the orb-weaver in no way fits the raft spider (G Arnqvist & Henriksson, 1997). Female fecundity was linked to abdomen size rather

than entire body size, as the size of the abdomen determined the quantity and density of eggs a female can hold (G Arnqvist & Henriksson, 1997). They found that females of a higher fecundity were more likely to cannibalize smaller males, but not due to how much food they had consumed (G Arnqvist & Henriksson, 1997). They tested this by starving females and feeding others freely and comparing mating attempts between the groups. Upon finding that there was no link in consumption of food and consumption of males, they looked to the life cycle of the fishing spider to explain the phenomenon (G Arnqvist & Henriksson, 1997). They hypothesize, rather soundly in terms of assumptions, that the female fishing spiders who are more aggressive during pre-adult stages will grow larger as they will survive and catch more food (G Arnqvist & Henriksson, 1997). Females who show a greater voracity earlier in life will in turn have more resources at their disposal and grow to a larger, healthier size. This larger size means they'll have a larger abdomen and more energy to put into egg production. The consumption of males though does not affect egg production, and the reason it persists through evolution is its not detrimental enough to the population to cause issues. Males still manage to reproduce, and since a high voracity adolescent female is still favored in an aggressive environment, the voracity has no major selective pressure against it in the adult stage. This aggressiveness may even be genetically linked so that it persists in the females that survive longer to produce more equally aggressive off spring, which is why the sexual cannibalism exists (G Arnqvist & Henriksson, 1997). This presents sexual cannibalism as clearly non-adaptive, since the female nor the male are gaining any sort of direct fecundity from the consumption of the male under this model.

The aggressive spillover hypothesis is further supported in another fishing spider species, as seen in a study on *Dolomedes triton* by Johnson. The study examines the fishing spider species under the light of the adaptive foraging hypothesis and the aggressive spillover hypothesis. Through the manipulation of food availability in both juvenile and adult spiders, Johnson found support for both hypotheses in the species, but a lot more evidence backing the aggressive spillover hypothesis came out of the study (J C Johnson, 2001). He found that highly voracious juveniles had an increased fecundity during their adult stages in comparison to females that were starved during their juvenile stage (J C Johnson, 2001). This supports Henriksson & Arnqvist's assertion that sexual cannibalism is simply a spillover from a life history period where it was advantageous to be aggressive towards anything rather than apprehensive to mates. Both of these studies though are still looking at different species than the original studies that looked at the adaptive foraging hypothesis. It would make sense that both species in the *Dolomedes* family might both fall into the aggressive spillover hypothesis given how closely related they are.

These studies all build on the idea that aggression, or rather voracity, is the primary reasoning as to why sexual cannibalism exists and still persists in spiders like the fishing spider. They show solid evidence that food does not really have an impact on fecundity (outside of general starvation side effects) in adult fishing/raft spiders as they have reached their maximum body size. They both give reasoning and further evidence that sexual cannibalism is simply a remnant of adolescent voracity that hasn't been selected against through evolution despite its seemingly negative nature. This clearly shows that the behavior could possibly be non-adaptive, at least in fishing/raft spiders.

So what is wrong with these hypotheses?

They don't take different organisms into account.

There is a lot of animosity in the research world when it comes sexual cannibalism given the diversity of research and hypotheses on the matter. Some papers though call out specific hypotheses and studies in an attempt to discount their evidence and claims, which is a bit hostile even. The Henriksson & Arnqvist study in particular clearly attempts to disprove the model proposed by Newman & Elgar. The main issue with the study is that instead of the orb weaving species used in the 1991 study, Henriksson focuses on the fishing spider, which aren't that closely related phylogenetically. It surmises to say that there are differences in their mating systems, affecting the way sexual cannibalism is manifested in each species. More time and effort seems to be placed in looking at saying their ideas are right rather the other study's before them. While more research isn't a bad thing, the research seems a bit misguided. More effort should be applied to studying sexual cannibalism in less studied organism like scorpions. Doing so would reveal new information, even if it does fit into the guidelines of a previously formulated hypothesis. Researchers should also look to compare the mating systems of various species with those of the species from the study they are comparing theirs to. Doing so may explain differences in results and manifestations of habits.

Species in the *Dolomedes* family are closely related, and the various orb-weavers that we've seen studied are closely related to one another as well. Interestingly enough we see that there a lot of similarities in how sexual cannibalism does or does not benefit these closely related species. There needs to be more focus and drive around these relationships rather than against them.

Really though, is it Adaptive or Non-Adaptive?

Yes and No.

The 1997 study by Andrade examined the Australian redback spider under the lens of the adaptive model. They found that the female redback spider was statistically more likely to cannibalize a male if the female was previously withheld food. This study, along with Newman & Elgar's study (Winkler & Hall, 2013), find that sexual cannibalism is adaptive for females. Andrade proposes that it may even be adaptive for male redback spiders as it increases their parental investment by bettering the health of the female. (Andrade, 1998). We also see this adaptive behavior in many other spider species including orb-weavers and black widows (Blamires, 2011; J. Chadwick Johnson et al., 2011; Newman & Elgar, 1991). Sexual cannibalism isn't just adaptive with certain spiders though, as I've illustrated it is adaptive in Mantids, and potentially just as adaptive in Scorpions (K. L. Barry et al., 2008; Lawrence, 1992; Lelito & Brown, 2006; Young et al., 1988). The mate choice hypothesis, though a bit more general in its nature, presents equal evidence that females are selecting the males with which they prefer to mate with instinctually and in turn cannibalizing the less desirable, or smaller, males (Kralj-Fišer et al., 2011; Persons & Uetz, 2005; Prenter et al., 2006).

On the equally backed flip-side, studies advocating for the aggressive spillover hypothesis like Arnqvist & Henriksson's study suggest that it's not at all adaptive for either sex, it's just a trait from pre-adult life that has persisted because there isn't enough selective pressure against it (G Arnqvist & Henriksson, 1997). Johnson's 2001 study (Johnson, 2001) that also examined the fishing spider found the trait to be potentially non-adaptive, as the aggressive spillover hypothesis was supported in more cases than adaptive foraging. While there are fewer major studies on the hypothesis, the studies that have been conducted have gathered concrete evidence that support their assumptions and claims based on the aggressive spillover hypothesis.

So Convergent Evolution then?

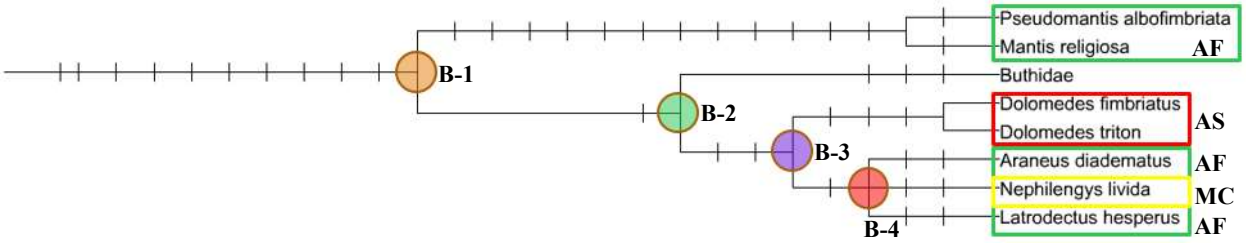

Figure 1. *A Phylogenetic tree containing various species of spiders, scorpions, and mantids that demonstrate sexual cannibalism. Each tick mark denotes an ancestor. AF denotes species fitting the adaptive foraging hypothesis. MC denotes species fitting the mate choice hypothesis. AS denotes species fitting the aggressive spillover hypothesis.*

Over the course of this chapter I've shown that the different hypotheses – adaptive foraging, mate choice, and aggressive spillover – all apply to different organisms, with some closely related species showing similar evolutionary reasons for sexual cannibalism to persist through time. The existence of sexual cannibalism can be both adaptive and non-adaptive, it really just varies with species. Interestingly, the similarities grow with closely related species. The western black widow (*Latrodectus hesperus*) and the orb-weavers (*Araneus diadematus*) both fit into the adaptive foraging model, only being a few ancestors down from their common ancestor. Looking at branch B-3, the raft spider (*Dolomedes fimbriatus*) is many ancestors apart from the most recent common ancestor with the western black widow, nephilid, and orb-weaver lineage. The western black widow, nephilid, and orb-weaver spiders are comparatively closely related to one another, as seen at branch B-4. This phylogenetic difference is reflected in that the raft and other fishing spiders all fit the aggressive spillover hypothesis for sexual cannibalism rather than the adaptive foraging. These differences in conjunction with the phylogenetic spread of the species could very well mean that the trait for sexual cannibalism evolved convergently in these organisms.

But that's not quite convincing enough one might think. There's also the fact that sexual cannibalism is seen in very distantly related members of the Arachnida class, scorpions. Scorpions are represented by the *Buthidae* family, as one of its member's exhibits sexual cannibalism. Branch B-2 shows an even greater phylogenetic difference than what was seen in the various spiders. Since there isn't a lot of focused research on the effects of sexual cannibalism in scorpions, it's hard to say if they fit a clear cut hypothesis that's already been laid out, but they are predicted to fit some form of the adaptive foraging hypothesis. Scorpion research may serve as a testing ground for my hypothesis of convergent evolution even,

comparing their life history and mating habits with those of their relatives displaying sexual cannibalism. Going even further in terms of relations though, there's the Insecta class, which is shown branching from the Arachnida class at branch B-1. At this point the most common ancestor is dozens of ancestors away for insects such as mantids from arachnids. Mantids are not as sexually dimorphic as their arachnid counterparts and as such sexual selection plays a bit of a different role in mating system, as I have shown in my mantid subsection. The fact that sexual cannibalism exists in this distant of a relative without being manifested in a common ancestor is further proof that these traits would have had to have evolved independently in most organisms.

Looking at sexual cannibalism as a convergently evolved trait allows for differences to exist between different organisms without one new organism's manifestation having to undermine an existing theory for another organism all together. Sexual cannibalism doesn't have a one size fits all hypothesis, but rather there needs to be a set of hypotheses constructed on a per organism basis with assumptions based on close relatives. With this system we can get closer to understanding why the sexual cannibalism may exist and why it persists even when it seems like it's maladaptive. Sexual Cannibalism is a vast, interesting topic and biologists have only scratched the surface of what it has to tell us about mating systems.

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