



## CURRENT ISSUES - PERSPECTIVES AND REVIEWS

# Challenging the Aggressive Spillover Hypothesis: Is Pre-Copulatory Sexual Cannibalism a Part of a Behavioural Syndrome?

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**Abstract**

Pre-copulatory cannibalism – females devouring males during courtship – may bring no benefit to either sex. The ‘aggressive spillover hypothesis’ (ASH) posits that pre-copulatory cannibalism represents a spillover of female aggressiveness from the juvenile foraging context, when aggressiveness is advantageous, to the adult mating context, when aggressiveness may be non-adaptive or maladaptive. The ASH suggests that individuals exhibit limited plasticity in aggressive behaviours because they are genetically canalised for indiscriminate aggressiveness towards prey and conspecifics, including males. Hence, a tendency to employ pre-copulatory cannibalism is a part of the female aggression syndrome, an assertion generally accepted in the personality field. We here re-evaluate the previous findings in the light of personality criteria, which we propose for ASH validation: between-individual differences, repeatability and heritability in tendency for pre-copulatory attacks (and pre-copulatory cannibalism) and voracity towards prey, and their correlation. To re-evaluate ASH and to allow for additional or alternative explanations, we ask whether pre-copulatory cannibalism depends on female hunger, mating status, size and/or male quality. Finally, we ask whether cannibalistic females have a reduced reproductive success as predicted by the ASH. While repeatability and heritability in voracity towards prey and its correlation with the tendency to engage in pre-copulatory cannibalism were found in certain systems, we lack any evidence for repeatability and heritability in pre-copulatory cannibalistic attempts and for its maladaptive-ness. Rather than only resorting to the ASH, foraging and mate choice hypotheses may also explain pre-copulatory cannibalism. We suggest clarifying the use of the terms *sexual cannibalism* (effect) and *female aggressiveness* or *tendency to attack and devour males* (cause), and argue that male strategies to avoid cannibalism should be considered. We propose testing the ASH as the explanation for pre-copulatory cannibalism in those cases where female tendency to devour males correlates with actual pre-copulatory cannibalism and when all the above criteria are fulfilled. Finally, we propose future directions for studying the ASH.

## Introduction

Sexual cannibalism, a phenomenon where females attack, kill and consume males before, during or after copulation, is taxonomically confined to insects (praying mantis), arachnids (spiders, scorpions) and amphipods (reviewed in Elgar 1992). It has been interpreted as a consequence of four non-mutually exclusive factors: failing recognition of a potential mate by voracious females (Gould 1984); mate choice, where females attack/devour unwanted mates (Elgar & Nash 1988; Elgar 1992; Persons & Uetz 2005; Prenter et al. 2006; Kralj-Fišer et al. 2012); hunger, when females benefit from the energy and nutrient intake by consuming the males (adaptive foraging hypothesis) (Newman & Elgar 1991; Snyder et al. 2000; Barry et al. 2008) or genetic constraints (aggressive spillover hypothesis) (Arnqvist & Henriksson 1997; Johnson & Sih 2005). Within the latter, sexual cannibalism is explained as a consequence of an aggressive personality or an aggression syndrome, implying that aggressive females are not able to flexibly modify their high level of aggressiveness across contexts, such as between foraging and mating (Sih et al. 2004).

The costs and benefits of sexual cannibalism depend on the sex as well as the timing of sexual cannibalism and the species' mating system (monogamous vs. polygamous) (Elgar & Schneider 2004). In those cases where males' fitness benefits of sexual cannibalism exceed the benefits of future matings, for example, in spiders with strict male monogamy, males may be selected for sacrificing their body during or after copulation (Andrade 1996, 2003; Schneider & Elgar 2001; but see Li et al. 2012). In a polygamous species, however, it may be in the male's interest to avoid female attacks (Barry et al. 2009; Roggenbuck et al. 2011). Sexual cannibalism during or after copulation may indeed benefit both sexes under certain circumstances (Birkhead et al. 1988; Elgar & Nash 1988; Andrade 1996; Moya-Larano et al. 2003; Prokop & Vaclav 2005; Barry et al. 2008). However, while pre-copulatory cannibalism may or may not entail advantages for females, it is always very costly to males. Therefore, pre-copulatory cannibalism has been viewed as one of the most extreme forms of sexual conflict (Buskirk et al. 1984). Due to high potential costs of pre-copulatory cannibalism for both sexes (i.e. reduced or no reproductive success for females; death and no paternity for males), it is difficult to explain its evolutionary persistence. Pre-copulatory cannibalism, therefore, is of considerable interest in exploring its behavioural correlates and adaptive consequences.

Females of the fishing spider, *Dolomedes fimbriatus*, reportedly exhibit an extreme, and peculiar, case of pre-copulatory cannibalism, where very aggressive females attack all males during courtship and thereby risk to remain unmated despite repeated male mating attempts (Arnqvist 1992; Arnqvist & Henriksson 1997). As such female behaviour yields no obvious net benefit to either sex, pre-copulatory cannibalism in this system has been interpreted to be non-adaptive or even maladaptive (Arnqvist & Henriksson 1997). To explain this evolutionary paradox, Arnqvist & Henriksson (1997) proposed the 'aggressive spillover hypothesis' (ASH), which posits that pre-copulatory cannibalism represents a carryover of female aggressiveness from the juvenile foraging context – where high levels of aggression are selectively favoured – to the adult mating context, when such behaviour becomes non-adaptive or maladaptive. From the proximate point of view, juvenile aggression carries over into the adult stage because of genetic constraints, which limit behavioural flexibility over time and across contexts (Arnqvist & Henriksson 1997). Indeed, aggression in territorial and foraging contexts has been shown to be heritable in numerous species, including arthropods (Riechert & Hedrick 1993; Kortet & Hedrick 2007; Pruitt et al. 2008; Kralj-Fišer & Schneider 2012; Kralj-Fišer et al. 2012). Furthermore, aggressiveness was found to be repeatable over time (Pruitt et al. 2008; Kralj-Fišer & Schneider 2012; Kralj-Fišer et al. 2012) and consistent across several contexts (Pruitt et al. 2008; but see Kralj-Fišer et al. 2012; Kralj-Fišer & Schneider 2012). Therefore, aggressiveness is considered a personality trait. The reasoning of ASH is that individuals exhibit only limited plasticity in aggressive behaviours because they are genetically canalised for indiscriminate aggressiveness towards prey and conspecifics including males. Hence, a tendency to employ pre-copulatory cannibalism is a part of a female aggression syndrome, and personality researchers seem to generally accept the ASH as an explanation for excessive pre-copulatory sexual cannibalism (Sih et al. 2004; Johnson & Sih 2005).

A behavioural syndrome occurs when individuals behave in a consistent way through time and/or across contexts (Sih et al. 2004; Bell 2007; Kralj-Fišer et al. 2010). Thus, a population exhibiting an aggression syndrome will be characterised by between-individual differences in aggressiveness, which remain stable over time and across different contexts (Kralj-Fišer et al. 2007, 2010). To explain pre-copulatory sexual cannibalism as a by-product of an aggression syndrome or an aggressive personality as suggested, one should show that (1) females consistently differ

in their aggression towards males resulting in different probabilities of pre-copulatory sexual cannibalism and in aggression in the foraging context (2) and that these two behaviours correlate. Furthermore, if an individual cannot modify its aggressive behaviours due to genetic correlations, (3) a high heritability of voracity towards prey and tendency for pre-copulatory sexual cannibalism should be expected.

### Empirical Evaluations of ASH

Below, we describe the findings of studies that tested the ASH and re-evaluate them in the light of the above criteria. Specifically, we seek evidence for (1) between-individual differences in pre-copulatory cannibalism and in voracity towards prey, (2) repeatability of these behaviours and (3) correlation between tendency to engage in pre-copulatory cannibalism and voracity towards prey. Furthermore, the ASH states that highly aggressive females exhibit larger adult body sizes and higher propensity for pre-copulatory cannibalism independent of their mating status, hunger level and mate quality (Arnqvist & Henriksson 1997). Hence, we look for (4) the correlation between female propensity for pre-copulatory cannibalism and her adult body size. To re-evaluate the support for the ASH and to allow for additional or alternative explanations, we ask whether (5) the incidence of pre-copulatory cannibalism depends on factors such as female hunger (if females reared under low food conditions, more often employ pre-copulatory cannibalism), mating status (if mated females more often employ pre-copulatory cannibalism) and/or mate quality (if females more often cannibalise less pre-

ferred male phenotypes). Finally, we ask whether (6) cannibalistic females have a reduced reproductive success as predicted by the ASH (Table 1).

### Pre-Copulatory Cannibalism in Fishing Spiders (*Dolomedes fimbriatus*, *D. triton*)

The ASH by Arnqvist & Henriksson (1997) ensued from the instances of pre-copulatory cannibalism in the fishing spider, *Dolomedes fimbriatus*. In this species, virgin females may attack and attempt to cannibalise males during courtship and mating (Gerhardt 1926; Schmidt 1953; Arnqvist 1992). Arnqvist & Henriksson (1997) reported that the high rate of sexual cannibalism in this protandric species results in dramatic declines of the male population when females mature. In laboratory trials with unknown sample sizes, they found that in 78% of partly repeated interactions, females attacked courting males from a distance (Arnqvist & Henriksson 1997). In 11% (Arnqvist & Henriksson 1997) or 3% (Arnqvist 1992) of such attacks, males were killed, resulting in a relatively low risk of sexual cannibalism at this stage of courtship (the actual numbers of killed males are not reported but can be estimated to be a single male in Arnqvist 1992). The male risk amounts to 7% at the next pre-copulatory stage, that is, during mounting of females (Arnqvist 1992). To explain these observations, the authors tested and excluded the effects of female mating status (the number of palpal insertions a female had received), male size, and food availability on aggressive behaviour of females (Arnqvist & Henriksson 1997). However, they found that smaller males were more likely

**Table 1:** Relationships to pre-copulatory cannibalism

Species	Aggressiveness in a foraging context (latency to attack prey)	Female mating status	Female adult size	Hunger state	Mate quality	Reproductive success
Theory (Arnqvist & Henriksson 1997)	Positive relationship	No relationship	Positive relationship	No relationship	No relationship	Negative relationship
<i>Dolomedes fimbriatus</i>	n.m.	No relationship	No relationship	No relationship	No relationship to body size	No relationship
<i>Dolomedes triton</i>	Positive relationship	n.m.	No relationship	n.m.	No relationship to body size	No relationship
<i>Anelosimus studiosus</i>	Positive relationship	n.m.	n.m.	n.m.	Aggressive females more likely cannibalise large aggressive males	Negative relationship
<i>Agelenopsis pennsylvanica</i>	Positive relationship	n.m.	No relationship	Positive relationship	No relationship to body size and mass	Positive relationship

N.m., not measured.

to be cannibalised after an attack, which might support the mate choice and the mate size dimorphism hypothesis (MSD) (e.g. Wilder & Rypstra 2008; Roggenbuck et al. 2011). The MSD hypothesis suggests that females are indiscriminately aggressive towards males, and that their actual killing depends on the female's physical strength relative to the male's ability to defend his life, which both depend on body size (Wilder & Rypstra 2008).

Arnqvist & Henriksson (1997) interpreted their findings on the fishing spider as follows: adult size depends on juvenile growth, and thus, juvenile food consumption should determine female fitness. Food consumption is positively related to foraging aggression, and hence, aggressive behaviour is selectively favoured during development. Aggressive juvenile females consume more prey, acquire larger adult sizes and should produce more offspring than non-aggressive juveniles. However, because of genetic constraints on aggressive behaviour, adult females exhibit high aggression and low discrimination towards prey including male conspecifics and may remain unmated; this reasoning led Arnqvist & Henriksson (1997) to develop the ASH as a conceptual model.

Unfortunately, the data on *D. fimbriatus* do not allow a direct estimation of the risk of remaining unmated because females are known to consume unfertilised egg batches, and hence, field samples of egg-carrying females are biased towards fertilised females (Arnqvist & Henriksson 1997). Suggestive evidence comes from 18 field-collected, egg-carrying females that were used to determine the fertilisation rate of their egg sacs (Arnqvist & Henriksson 1997). All egg sacs contained fertilised eggs, but in a third of the inspected clutches, fertilisation rates were below 50%. It is possible that the latter group of females received only one palpal insertion, plausibly due to female aggression (Arnqvist & Henriksson 1997). Hence, the reason for the low fertilisation rates is based on the authors' assumption (Arnqvist & Henriksson 1997), not data, and so the actual costs of female aggressiveness remain unknown. Furthermore, it is unknown how these fertilisation rates compare with the rates in other, less cannibalistic species.

To further complicate the outcomes of the study, only a small proportion of the experimental females laid eggs (Arnqvist & Henriksson 1997). Causes for reproductive failure are dubious but at least six females received no copulation although it is not clear whether this was due to female aggressiveness (Arnqvist & Henriksson 1997). If more than 80% remained unmated, this would contradict personality theory

assuming high between-individual variability in personality traits (e.g. Koolhaas et al. 1999). However, it is possible that the experimental conditions including the males' options to escape or the observation duration of only 45 min might be at least partly responsible for the observed low mating success and/or high cannibalism frequencies. In cannibalistic species, males often approach females very cautiously, and it may take more than an hour for copulation to occur, as for example, in *Dolomedes triton* (Johnson & Sih 2005), in *Argiope keyserlingi* (Herberstein et al. 2002) and the redback spider (Stoltz & Andrade 2010; Neumann & Schneider 2011). Also, copulation latency might be longer for aggressive vs. non-aggressive females, as, for example, in *Anelosimus studiosus* (Pruitt & Riechert 2009a). Hence, if a realistic risk of sexual cannibalism is to be estimated, mating trials should allow sufficient time. Although males in this study commenced courtship early during trials, over 70% were attacked from a distance. Although most of them successfully evaded female attack, they may subsequently become particularly cautious and require even more time and space for another approach (Arnqvist & Henriksson 1997). Furthermore, even though the ASH predicts reduced reproductive output, Arnqvist & Henriksson (1997, p. 259) found no difference between cannibalistic and non-cannibalistic females in this respect.

Foraging success will generally result in larger size and weight, and females' larger size and weight results in higher fecundity, a correlation that has been shown in many insect and spider species (Higgins 1992; Spence et al. 1996). Arnqvist & Henriksson (1997) did not directly measure aggressiveness in foraging but predicted that fecundity selection for large female body size would also favour high aggressiveness towards prey as this will increase foraging success. Johnson & Sih (2005) directly tested aggressiveness in a foraging and mating context in a congener, the American fishing spider, *D. triton*. As predicted by the ASH, *D. triton* females exhibited consistent individual differences in aggressiveness towards prey through ontogeny, which suggests a genetic control of aggressive behaviours in the foraging context (Johnson & Sih 2005). Unfortunately, the authors did not control for female hunger – but should – to test the ASH. Voracity towards prey should generally be compared between individuals of the same state and motivation (age, sex, hunger level and mating status). Nevertheless, in accordance with the ASH predictions, aggressiveness towards prey correlated positively with feeding rate, adult size and fecundity (Johnson & Sih 2005). The authors report a



positive correlation between voracity in foraging and the tendency to engage in pre-copulatory attacks. Moreover, 46% of the males that were attacked (attacks occurred in 32% of all courtship events across the whole experiment) were killed in pre-copulatory attacks, and a female's propensity to kill and consume a male was well explained by her tendency to engage in pre-copulatory attacks. Surprisingly, the same measure of aggressiveness was not correlated with the number of palpal insertions she ultimately received or to the fertilisation rate of her egg sac, suggesting aggressive females did not suffer reproductive costs (Johnson & Sih 2005). Hence, while the predictions of the spillover model hold in the system, the presumed costs of pre-copulatory sexual cannibalism to females were not present. Interestingly, consuming one or more males had no effect on female fecundity, which suggests that pre-copulatory sexual cannibalism entails neither costs nor benefits to females.

To sum up, the ASH has a good potential to explain the high frequency of pre-copulatory sexual cannibalism in fishing spiders (genus *Dolomedes*). However, as pointed out by Johnson & Sih (2005) and by Arnqvist & Henriksson (1997), longitudinal studies would be called for as well as heritability estimates. Furthermore, realistic estimations of the true frequencies and costs of pre-copulatory sexual cannibalism to females are highly desirable.

#### Pre-Copulatory Cannibalism in a Subsocial Spider (*Anelosimus studiosus*)

To some degree, studies of *A. studiosus* support the ASH as an explanation of pre-copulatory cannibalism. These subsocial spiders are polymorphic in social (aggressive) behaviours (Pruitt et al. 2008). The findings that social females are consistently less aggressive towards predators and prey and less often cannibalise males during courtship than aggressive females (7.5% vs. 30%; (Pruitt & Riechert 2009a,b; Pruitt et al. 2008, 2011) are in accordance with the ASH predictions. In line with the ASH, docile females exhibit higher reproductive output and are preferred by males over aggressive females (Pruitt & Riechert 2009a). Other results may or may not support the ASH. In the staged experimental trials, successful copulation significantly more often occurred between aggressive and docile phenotype (aggressive female–docile male; aggressive male–docile female) than between two aggressive or two docile types (Pruitt & Riechert 2009a). However, aggressive females are more likely to kill large aggressive than small docile males, which is adaptive; this pair combination has an

increased reproductive success (Pruitt et al. 2011). It is possible that aggressive females use sexual cannibalism as a mate choice strategy, when they preferentially reject and devour large aggressive males. Furthermore, the latency to copulate is longer in aggressive females, which may further support the notion that aggressive females are choosier than social ones (Pruitt & Riechert 2009a). Alternatively, males may be more cautious when attempting to copulate with aggressive females. These questions remain open. In summary, sexual cannibalism in *A. studiosus* is not an invariant element within a broader syndrome, and hence, it cannot be considered merely a spillover of aggressive personality, but it seems to be a result of interaction between social and sexual selection (Pruitt et al. 2011).

#### Pre-Copulatory Cannibalism in a Funnel Spider (*Agelenopsis pennsylvanica*)

As in the above studies, pre-copulatory cannibalism in a funnel spider, *A. pennsylvanica*, could not be solely explained by the ASH (Berning et al. 2012). Pre-copulatory cannibalism occurred in 36% of all matings of virgins; however, none of the tested females killed two males in succession (Berning et al. 2012). The females that killed the first male, later copulated with the second male (Berning et al. 2012). The authors showed that pre-copulatory cannibalism in *A. pennsylvanica* depended on the female's general aggressiveness, measured as voracity towards prey, as well as on hunger state: the most aggressive females, and those deprived of food, were most likely to consume their mates. These results suggest that pre-copulatory cannibalism in this system can be explained with the ASH and with a foraging strategy. In contrast to the ASH predictions, however, virgin females that consumed the first potential mate prior to copulation, exhibited increased reproductive success: they gleaned more offspring from heavier egg sacs (Berning et al. 2012). This study clearly demonstrates the adaptive consequences of pre-copulatory sexual cannibalism, which can be a result of multiple mechanisms acting in concert.

Furthermore, despite females exhibiting consistent individual differences in aggression in the foraging context, the fact that females never cannibalised two males consecutively implies the lack of repeatability of pre-copulatory cannibalism. These results contradict the ASH and instead suggest that pre-copulatory cannibalism might be related to mate choice. However, pre-copulatory cannibalism was independent of male size and mass. To further investigate mate choice

and foraging as explanations, we believe that further experiments should test for other male qualities such as aggressiveness and courting intensity (Pruitt & Riechert 2009a; Pruitt et al. 2011; Kralj-Fišer et al. 2012), in particular because females that rejected the first male had higher reproductive success. To conclude, pre-copulatory cannibalism in *A. pennsylvanica* may be explained as a foraging strategy and partly by the ASH – voraciousness levels of virgin females were positively related to incidences of pre-copulatory cannibalism in their first mating trial.

## Future Directions

### Semantics & Conceptual Pitfalls

First, we find it crucial to clarify the use of the terms *sexual cannibalism* (effect) and *female aggressiveness or tendency to attack and devour males* (cause). These terms should not be used interchangeably as sexual cannibalism is a possible but not the sole consequence of female aggression. Indeed, there are several examples where females behave aggressively towards males, but if the male continues to court, copulation may still occur with or without a subsequent cannibalism event (Wilder & Rypstra 2008; Roggenbuck et al. 2011; Kralj-Fišer et al. 2012; 2013). Furthermore, sexual cannibalism is not solely dependent on female behaviour; it depends also on male behaviour and on mate size differences (Wilder & Rypstra 2008). A more suitable terminology in studies of the ASH and female personality would be to use 'tendency to attack a courting male' in place of 'pre-copulatory cannibalism'. Additionally, male behaviour and male personality need to be considered. Males have evolved strategies to circumvent the mortality risk, for example, through opportunistic mating (Robinson & Robinson 1980; Kuntner et al. 2009a,b), remote copulation (Li et al. 2012) or may vary in their risk to fall victim to the female even in the absence of specific counter-strategies (Arnqvist & Henriksson 1997; Roggenbuck et al. 2011). Indeed, research on spider courtship suggests that females use aggressive behaviour to test the persistence of males, and male persistence may ultimately result in copulation (Pruitt & Riechert 2009a; Kralj-Fišer et al. 2013).

A study that attempts to test the ASH should (1) establish whether there is a repeatability and heritability of relevant behaviours, and if female tendency to attack a courting male, the frequency of sexual cannibalism and adult size correlate positively (e.g. Johnson & Sih 2005) and/or (2) stage mating trials of sufficient length to allow for copulation after several

attacks, and observe concrete incidences of pre-copulatory cannibalism. Mating trials should also assess the percentage of females that remain unmated and ideally, experimental findings should be supported with field observations (e.g. Arnqvist & Henriksson 1997), perhaps in comparison among differently cannibalistic species. Such data are needed to determine whether female adult aggressiveness may indeed be maladaptive in a mating context.

Because of the latter ASH condition, it is not clear how to estimate behavioural heritability – a crucial element of personality – in females with the highest aggression level if they will devour all potential mates, remain unmated and thus have no offspring that could inherit their personality. The paradox in need of explanation is then how extreme aggressiveness can persist when highly aggressive females indeed leave no offspring. However, the observation/assumption that highly aggressive females suffer costs of remaining unmated is not well supported to date and is further challenged, at least in spiders, by the perhaps underestimated frequencies of 'opportunistic mating'. This term is used to describe a male strategy to copulate with defenceless (feeding or moulting) females. Teneral females are particularly vulnerable to opportunistic mating because they are incapable of any resistance (Robinson & Robinson 1980; Kuntner et al. 2009a,b). Hence, in invertebrates that mature through final moulting, even the most aggressive females that possess the drive to cannibalise their mates are unable to do so while moulting (Robinson & Robinson 1980). Opportunistic mating thus ensures that even the most aggressive females still reproduce. Future studies should pay attention to and measure the occurrence of opportunistic mating in the study species.

### Proposed Experiments

While most existing studies focused on a single aspect of the ASH, we lack a comprehensive study (see also Arnqvist & Henriksson 1997). Here, we propose an experiment designed to test the concept holistically. As a basic requirement, it is important that the study females are virgin and well (equally) fed and that males are of similar genetic quality, for example, using brothers in a replicated split-brood design. The influences of female mating status and hunger and undesired mate choice effects would thus be reduced and/or controlled.

The ASH assumes that the tendency to devour potential mates is genetically determined. Testing for heritability is therefore important, and the above problems need to be considered and overcome. One

option to resolve this problem is to create situations for opportunistic matings and/or to mate aggressive females with aggressive males and prevent sexual cannibalism (e.g., Herberstein et al. 2011). Then, daughters of such females should be tested for their tendency to attack a courting male.

To experimentally account for potential male influence, we propose to test several groups of sisters for voracity towards prey and brothers for intrasex aggressiveness. Unrelated pairs should then be subjected to mating trials and be matched for aggressiveness type; half of the sisters should be examined when adult, whereas the other half should be subjected to a male during moulting. Then, occurrences of pre-copulatory cannibalism and reproductive output between females of different voraciousness could be compared. Moreover, heritability of tendency to attack and devour potential mates could be estimated.

The ASH explains the phenomenon that virgin females cannibalise males prior to copulation, thereby reducing their own reproductive output by a genetic correlation of aggressiveness across two contexts. A recent meta-analysis of 11 vertebrate and invertebrate species indeed revealed that genetic correlations underlying behavioural syndromes, such as the aggressiveness syndrome, have the potential to significantly constrain evolutionary responses (Dochtermann & Dingemanse 2013). Other examples show that occurrence of a behavioural syndrome may vary depending on the presence of a direct selective force. For example, in the three-spined stickleback (*Gasterosteus aculeatus*), differences in predation pressure between closely related populations correspond to differences in behavioural correlations between aggressiveness, activity and exploratory behaviour (Dingemanse et al. 2007). Behavioural correlations were found in populations that co-occurred with aquatic predators but not where the predator was absent (Dingemanse et al. 2009).

A genetic approach towards investigating the behavioural correlation was already suggested (Arnqvist & Henriksson 1997). It would be interesting to test whether the assumed genetic correlation underlying pre-copulatory sexual cannibalism is stable or can be broken through changes in selection regimes. A possible approach would be the use of selection experiments (Beldade et al. 2002; Conner et al. 2011). Conner et al. (2011) showed that genetic correlations can be broken in fewer than 10 generations. It is unknown whether a correlation between voracity towards prey and aggressiveness towards mates may be due to pleiotropy or linkage disequilibrium between linked loci (Futuyma 2005). Nevertheless,

such an experiment should be doable in a spider species in which voracity towards prey is a heritable trait and in which the voracity towards prey correlates with the tendency to attack and devour a potential mate. Using a full-factorial design, females of similar aggressiveness should undergo four selection treatments: 25% should be reared and mated in conditions with few mates and plenty of food (A); 25% of the females in low mate availability and low food conditions (B); 25% of the females in high mate availability and low food conditions (C); and 25% of the females in high mate availability and high food conditions (D). After each generation, the females of the four selection lines could be tested for their aggressiveness in both, foraging and mating contexts. If artificial selection can break the genetic correlation, we expect to find a lower percentage of cannibalistic females in the selection line A compared with the selection line C. It is difficult to predict the results of the selection lines B and D.

## Conclusions

We suggest using the ASH as the explanation for pre-copulatory cannibalism only in those cases where female tendency to devour males correlates with actual pre-copulatory cannibalism (e.g. Johnson & Sih 2005) and when all above criteria are fulfilled. While repeatability and heritability in voracity towards prey and its correlation with tendency to engage in pre-copulatory cannibalism were found in certain systems, we lack the evidence for repeatability and heritability in pre-copulatory cannibalistic attempts and cannibalism and for their maladaptiveness measured as reduced reproductive output or even the absence of mating in highly aggressive females. However, while the ASH explains pre-copulatory cannibalism solely based on female aggressiveness, we conclude that other factors may work in concert with personality, such as female hunger level (Wilder & Rypstra 2008, 2010; Wilder et al. 2009; Roggenbuck et al. 2011; Berning et al. 2012), mate size dimorphism (Roggenbuck et al. 2011), and mate behaviour and quality (Persons & Uetz 2005; Kralj-Fišer et al. 2012). Almost every study leaves the latter explanation, namely an extreme form of mate rejection, open. We thus encourage future studies to weigh the evidence for sexual selection as well.

In conclusion, it is well established that spiders exhibit differences in aggressive personalities; however, it remains open in what species aggressive behaviour in a foraging context spillover into mating context, and if/what additional factors are involved in pre-copulatory cannibalism. Furthermore, while

aggressive spillover has been indeed found in some species, we still need the evidence of its maladaptive consequences.

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