Mate choice and sexual size dimorphism, not personality, explain female aggression and sexual cannibalism in raft spiders

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Intersexual agonistic encounters prior to mating are thought to result from the 'spillover' of the advantages of a voracious personality within a foraging context that is maladaptive in a mating context. We tested this idea by examining the repeatability and cross-context consistency of aggressive behaviours associated with foraging and mating in the raft spider, *Dolomedes fimbriatus*, in which some, highly voracious females reportedly kill approaching males and thus remain unmated. We failed to find support for a maladaptive spillover of voracious female personality. While females exhibited consistent interindividual differences in voracity towards prey, voracity did not correlate with female aggressiveness towards males. Instead, we show that female *D. fimbriatus* adjusted their tendency to attack courting males according to their size relative to the male. Females commonly attacked males during or after copulation, but sexual cannibalism depended on relative mate size difference, with mating success tending to be compromised in females with lower body weight.
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Personalities, interindividual differences in behaviour that persist through time and across context, are observed across the animal kingdom (Kralj-Fišer & Schuett, 2014; Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Several studies report that individuals cannot flexibly adjust their behaviour to various contexts (Johnson & Sih, 2007; Quinn & Cresswell, 2005; Sih, Kats, & Maurer, 2003) implying that individuals do not necessarily respond optimally in a given situation (Bell, 2007; Sih, Bell, & Johnson, 2004). For example, bolder individuals have limited capacity to adjust their high tendency to express risk-taking behaviour when exposed to predators (Sih et al., 2003).

Among the earliest application of the 'suboptimal behavioural flexibility' idea was to explain premating sexual cannibalism (Arnqvist & Henriksson, 1997), in which the female captures and consumes her courting male prior to insemination (reviewed in Elgar, 1992). Clearly, the behaviour is potentially fatal for the male,

and selection is expected to favour male traits that mitigate against this risk (Elgar, 1992; Li, Oh, Kralj-Fišer, & Kuntner, 2012). The behaviour may also be costly for virgin females, which risk remaining unmated, and several benefits have been suggested, including foraging (Barry, Holwell, & Herberstein, 2008; Newman & Elgar, 1991; but see Wilder & Rypstra, 2010) and mate choice (Elgar & Nash, 1988; Elgar & Schneider, 2004; Kralj-Fišer et al., 2011; Prenter, MacNeil, & Elwood, 2006). Alternatively, the behaviour may reflect limited plasticity in aggressiveness (Arnqvist & Henriksson, 1997; Johnson & Sih, 2005).

The aggressive spillover hypothesis derives from the idea that female aggressive behaviours have limited plasticity, and was originally based on the behaviour of the raft spider, *Dolomedes fimbriatus*, Pisauridae, in which highly voracious females attack all males during courtship and remain unmated despite repeated male mating attempts (Arnqvist, 1992; Arnqvist & Henriksson, 1997; Morse, 2004). The excessive female aggression in the mating context is not beneficial per se to either sex. Arnqvist and Henriksson (1997) suggested that female aggressiveness from the juvenile foraging context, in which high levels of indiscriminate aggression are selectively favoured, spills over into the adult mating

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context, when such behaviour is not adaptive. An individual's aggression level exhibited during the juvenile stages persists into adulthood because of genetic constraints, which may limit the degree to which aggressiveness varies independently over time and across contexts (Arnqvist & Henriksson, 1997). In other words, the tendency to attack a male during courtship is associated with female personality: females are purportedly unable to adjust their aggression levels to be optimal in different contexts (e.g. Sih et al., 2004).

Dolomedes fimbriatus is often used as an exemplar of 'suboptimal behavioural phenomena' as a consequence of limited behavioural plasticity across different contexts (e.g. Bell, 2007; Sih et al., 2004). Arnqvist and Henriksson (1997) proposed, but did not test, the underlying assumptions of the aggressive spillover hypothesis. Following further investigations of precopulatory cannibalism in diverse spiders, including *Dolomedes triton* (Johnson, 2001; Johnson & Sih, 2005), *Anelosimus studiosus* (Pruitt & Riechert, 2009a, 2009b; Pruitt, Riechert, & Harris, 2011; Pruitt, Riechert, & Jones, 2008) and *Agelenopsis pennsylvanica* (Berning et al., 2012), Kralj-Fišer, Schneider, and Kuntner (2013) established the following evidence required to support the aggressive spillover hypothesis: (1) limited plasticity of foraging aggression over ontogeny and consistency in female aggression towards males during courtship in adult females; (2) limited plasticity of aggression across contexts, i.e. correlation between foraging aggression and female aggression towards males during courtship; (3) female aggression towards males independent of male traits; (4) female aggression towards males independent of the female's foraging history; and (5) reduced reproductive output of aggressive females (see also Johnson, 2013; Pruitt & Keiser, 2013).

Most studies reveal consistent individual differences in foraging aggression and positive correlations between foraging aggression and sexual cannibalism (Berning et al., 2012; Johnson & Sih, 2005; Pruitt et al., 2008; see also Khadka & Foellmer, 2013; Rabaneda-Bueno, Aguado, Fernández-Montraveta, & Moya-Laraño, 2014). However, none tested for the repeatability of female aggression towards males during courtship and its correlation with foraging aggression. These are crucial data because sexual cannibalism (in contrast to female aggression towards a male) does not depend exclusively on female behaviour; it is the outcome of both male and female behaviour (see also Wilder, Rypstra, & Elgar, 2009), with males typically attempting to evade being killed (see more in Kralj-Fišer et al., 2013). In contrast to aggressive spillover hypothesis predictions, the quality of male *A. studiosus* may play an important role in the female's decision to devour or mate with him (Pruitt et al., 2011; Pruitt & Riechert, 2009b), whereas female hunger in *A. pennsylvanica* seems to enhance sexual cannibalism (Berning et al., 2012; see also Schneider & Elgar, 2002). Finally, only aggressive *A. studiosus* females exhibited lower reproductive output (but they still mated) compared with less aggressive females (Pruitt et al., 2011; Pruitt & Riechert, 2009a), whereas cannibalistic *A. pennsylvanica* females had more and heavier offspring than noncannibalistic ones (Berning et al., 2012).

In this study, we revisited the aggressive spillover hypothesis for *D. fimbriatus* by explicitly testing the model's predictions. We asked whether differences in female aggressive behaviours remain consistent across different contexts and, in particular, whether aggressiveness in the foraging context spills over into the mating context. First, we made repeated observations of females within two different foraging situations to test for consistent individual differences in voracity over ontogeny. We exposed a subset of adult females to two mating trials to test for repeatability of aggressive behaviours towards males as well as repeatability of tendencies toward pre- and postcopulatory cannibalism. To examine context generality of aggressive behaviours we also observed aggression by

juvenile females towards a smaller conspecific. Further, we asked whether voracious females indeed remain unmated, by exposing a subset of females to up to five mating trials or until they copulated. Finally, we investigated whether copulation success is related to female body weight, and whether female aggression, copulation and cannibalism are associated with male quality, measured as absolute male body weight and relative male to female weight.

METHODS

Study Species

Dolomedes fimbriatus is a semiaquatic European species that occupies habitats close to water bodies, such as bogs, wet grasslands and woods. Adult females are marginally larger than males, and occur throughout the year, whereas adult males occur between March and November. *Dolomedes fimbriatus* feeds on invertebrates on the water surface or in vegetation, but retreats underwater when threatened. Our observations and previous studies (Arnqvist & Henriksson, 1997) indicate that *D. fimbriatus* probably exhibits a polygamous mating system. However, while males in our study were regularly observed to remate several times, only one female (3.45%) copulated repeatedly (see Results). Mated females carry their eggsacs in their chelicerae, but incorporate them into a nursery web prior to offspring emergence (Arnqvist, 1992; Schmidt, 1957).

We collected juvenile and subadult spiders along the Studena stream and nearby wet grassland near Malo Mraševo (Slovenia) between November 2013 and February 2014. The spiders were placed in individual terraria (35×25 cm and 10 cm high), and maintained in the laboratory (21 °C, 12:12 h dark:light regime). Each terrarium was filled with sufficient water to create a shallow pond that surrounded a small dry 'island'. We fed the spiders with two prey items (flies, crickets or mealworms) twice a week. We controlled for hunger levels in all trials, by not feeding the individual for a day prior to the trial.

Testing Individual Aggressive Behaviours

Each female was evaluated, as a juvenile and as an adult, for aggressiveness in several contexts. We first evaluated female foraging aggression in two ways: a 'voracity test', in which we dropped a live fly on the surface of the shallow water approximately 5 cm from a focal individual and measured her latency to attack the fly; and a 'foraging activity', in which we placed three live flies onto the inside wall of her terrarium and noted the number of flies killed within 1 h. In the few cases in which the fly/flies drowned during the test, we discarded the experiment. We evaluated aggression towards conspecifics by introducing a smaller conspecific into the terrarium of a juvenile female ($N = 64$ females; age: median = 11.5, first quartile (Q1) = 6, third quartile (Q3) = 37.25 days before maturity), and recorded their latency to attack within 300 s. A focal conspecific was at least 1.3 times heavier than a smaller conspecific (median = 1.68, Q1 = 1.37, Q3 = 2.08). In the next step, we performed mating trials; at the first trial all females were virgin. We examined the response of the adult females to courting males by gently placing a male into a female's terrarium, as far as possible from the female (35–40 cm). During the next 100 min, we noted whether: the male courted the female; the female reacted aggressively; the female cannibalized the male before or after copulation; and whether copulation took place. We defined female aggression as behaviour where the female chased (i.e. when she ran after a retreating male) or attacked (i.e. when she jumped on the male and/or bit him), but did not kill the male. If the female successfully killed the male, we quickly removed his body from her chelicerae. Males and females were weighed after the trial using an

electronic balance to an accuracy of 0.001 g. Thereafter we term the ratio between female and male body weight as sexual size dimorphism.

Our intention was to subject each female to the same number of trials in each test, but this was not possible. For the voracity test, 80 females were tested at least twice (on average 2.6 ± 0.6 trials per individual). The median female age at the first repeat was 5 days before maturity ($Q1 = 33$ days before maturity, $Q3 = 3$ days after maturity). The median interval between testing the same individual was 10 days ($Q1 = 7$, $Q3 = 14$). For the foraging activity test, 81 females were tested at least twice (on average 2.6 ± 0.7 trials per individual). At the first repeat the females' median age was 4 days before maturity ($Q1 = 32$ days before maturity, $Q3 = 3$ days after maturity). The median interval between testing the same individuals was 7 days ($Q1 = 4$, $Q3 = 10$).

We established two groups for the mating trials: in one, each female ($N = 47$) was tested up to five times or until she mated; and in the second, each female was observed in two mating trials ($N = 29$) regardless of whether she mated the first time. We used these data to test behavioural repeatability over two mating trials (age at the first trial: median = 4, $Q1 = 2$, $Q3 = 14$ days after maturity; days between mating trials: median = 2, $Q1 = 1$, $Q3 = 7$). However, those females that remained unmated after the second mating were subsequently tested again with up to three additional males. These data were combined with data of females from the first group to analyse behavioural correlates and potential reproductive costs of voraciousness. While females were never repeatedly paired with the same male, males were reused up to four times. In all staged mating trials, males were observed courting the female as described in Arnqvist (1992).

Ethical Note

Research on *D. fimbriatus* is not restricted by the animal protection law in the country where the study was performed. In the field we collected the minimal number of individuals needed to conduct the research. Spiders were kept in circumstances resembling their natural environmental conditions, i.e. in individual terraria with constant water availability, a dry 'island' and walls for attachments. The spiders were regularly fed with diverse prey items. The study was based on behavioural observations and all the experiments were noninvasive. After the experiments the spiders remained in the laboratory and reared as described above until natural death.

Statistical Analyses

Where appropriate, data were $\log(x+1)$ transformed to improve distributions. In the first step, we used generalized estimating equations (GEEs) to test for the effects of subsequent repeated trials (hereafter repeats), age at each test and their interactions on the voracity towards prey and foraging activity. To test the effects of potential confounding factors on behaviours observed in the mating context (mating occurrence, pre- and postcopulatory aggression, pre- and postcopulatory cannibalism) we also tested for the effect of female mating status. In GEE analyses we used ID as a subject variable, repeat as a within-subject variable and factor, and age as a covariate. To test for the potential effects on the behaviours observed in the mating context we added additional covariate = mating status (virgin, mated). We used the exchangeable working correlation matrix in all GEE analyses. For voracity towards prey, foraging activity and aggressive behaviours in the mating context we used linear, Poisson loglinear and binary logistic type of models, respectively.

To assess repeatability of individual behavioural differences tested in the foraging context we first checked for interindividual variability using the quartile variation coefficient formula: $V = 100 \times \frac{Q3 - Q1}{Q3 + Q1}$. In the case of binomial data taken in the mating trials we assumed that females exhibit interindividual differences when the same response (aggressive, nonaggressive) was shown by more than 30 or by fewer than 70% of females. While females exhibited considerable interindividual variation in voracity towards prey, foraging activity and precopulatory aggression, we found very low interindividual variation in their latencies to attack a smaller conspecific ($V = 0$), precopulatory cannibalism, postcopulatory aggression and postcopulatory cannibalism (see Results). Voracity towards a smaller conspecific, precopulatory cannibalism, postcopulatory aggression and postcopulatory cannibalism were therefore discarded from the repeatability analyses.

To calculate repeatability estimates we applied a mixed-effect modelling framework in order to estimate sources of variation in behaviour within and between individuals (Dingemanse & Dochtermann, 2013). We analysed repeatability values in R (version 2.15.3, Team, R. C., 2013) using rptR (Nakagawa & Schielzeth, 2010) and MCMCglmm packages (Hadfield, 2010). To calculate agreement repeatability (sensu Biro & Stamps, 2015; Nakagawa & Schielzeth, 2010) of voracity towards prey (continuous data) we used linear mixed-effects model (LMM) fitted by REML (restricted maximum likelihood); R function = rpt.remlLMM (behaviour, ID) (Nakagawa & Schielzeth, 2010). We estimated the repeatability of precopulatory aggression (binomial data) using GLMM (generalized linear mixed-effects model) with Poisson error structure and log-link function; R function = rpt.binomGLMM.add (behaviour, ID) (Nakagawa & Schielzeth, 2010). Foraging aggression was affected by repeat and repeat $*$ age (Table 1). Consistency in foraging activity was estimated as (1) agreement repeatability, which we calculated through generalized linear mixed-effects models fitted by PQL (penalized-quasi likelihood) estimation for binary data on the log-link scale; R function = rtp.pois.GLMM.multi (behaviour, ID), and as (2) adjusted repeatability (sensu Biro & Stamps, 2015; Nakagawa & Schielzeth, 2010) using MCMCglmm (Markov chain Monte Carlo linear mixed models) with Poisson variance distribution and uninformative priors (Hadfield, 2010; Nakagawa & Schielzeth, 2010; Wilson et al., 2010). To decompose phenotypic variance to within- and between-individual components, we included individual as a random effect in the model. We controlled the variance components for test sequence in the model (as fixed effect) and calculated the adjusted repeatability with 95% confidence interval according to Nakagawa and Schielzeth (2010).

We tested for cross-contextual correlates of individuals' aggressive behaviours using data from females that were tested in at least two different contexts. We ranked the data for voracity towards prey and foraging activity within each repeat, and then used the mean individuals' ranks over the repeats (mean ranks in voracity towards prey, mean ranks in foraging activity) for further analyses. We analysed the correlations across the two foraging situations (voracity towards prey and foraging activity) using Spearman's rho correlation coefficient (r_S). To test for correlations between female foraging aggressiveness in the foraging context and female aggressiveness towards males in the mating context we used logistic regressions (see Table 2). We used female aggressiveness data from the first mating trial, in which all females were virgin. To estimate the effect of sexual size dimorphism on mating occurrences and female aggression towards males we added the ratio female weight:male weight as an independent factor.

Finally, we used logistic regression to examine which independent variables (voracity towards prey, female weight) explained the differences between females that remained unmated after five mating trials and females that (eventually) copulated. Owing to the small number of unmated females, we performed bootstrapping (1000 samples). All analyses, except repeatability estimations (see

Table 1
The results of the generalized estimating equations testing for the effects of independent variables (factors) on behaviours (dependent variables)

Behaviour	Factors	Wald chi-square	df	P
Voracity towards prey (N=72)	Repeat	2.559	3	0.465
	Age	0.394	1	0.530
	Repeat∗age	6.266	3	0.099
Foraging activity (N=76)	Repeat	12.373	3	**0.006**
	Age	0.002	1	0.961
	Repeat∗age	24.286	3	**<0.001**
Mating (N=29)	Repeat	1.066	1	0.3028
	Age	1.858	1	0.173
	Repeat∗age	1.1432	1	0.285
	Mating status	3.784	1	0.052
Precopulatory aggression (N=29)	Repeat	0.066	1	0.797
	Age	0.326	1	0.568
	Repeat∗age	0.060	1	0.807
	Mating status	0.516	1	0.472
Precopulatory cannibalism (N=29)	Repeat	0.852	1	0.356
	Age	2.773	1	0.096
	Repeat∗age	3.783	1	0.052
	Mating status	0.829	1	0.362
Postcopulatory aggression (N=24)	Repeat	0.051	1	0.822
	Age	2.940	1	0.086
	Repeat∗age	0.234	1	0.629
	Mating status	1.227	1	0.268
Postcopulatory cannibalism (N=24)	Repeat	0.286	1	0.593
	Age	0.257	1	0.612
	Repeat∗age	0.274	1	0.600
	Mating status	0.316	1	0.574

In all analyses we used ID as a subject variable, repeat as a within-subject variable and factor, and age as a covariate. For testing the behaviours observed in the mating context we added additional covariate = mating status (virgin, mated). We always used the exchangeable working correlation matrix. For voracity towards prey, foraging activity and aggressive behaviours in the mating context we used linear, Poisson loglinear and binary logistic type of models, respectively. Significant results are in bold.

Table 2
The results of logistic regression tests

Dependent variable	Independent variables	B	SE (B)	Wald	P
Mating (N=69)	Voracity towards prey	−0.037	0.026	2.073	0.150
	Foraging activity	0.0017	0.018	0.005	0.946
	Male / female weight	1.114	2.107	0.279	0.597
	Precopulatory aggression	−1.680	0.611	7.560	**0.006**
	Constant	0.164	1.665	0.010	0.922
Precopulatory aggression (N=69)	Voracity towards prey	0.008	0.025	0.010	0.752
	Foraging activity	−0.011	0.018	0.364	0.546
	Male / female weight	4.268	2.130	4.015	**0.045**
	Constant	−3.092	1.685	3.366	0.066
Precopulatory cannibalism (N=69)	Voracity towards prey	0.017	0.035	0.242	0.622
	Foraging activity	0.003	0.029	0.011	0.918
	Male / female weight	0.253	3.338	0.006	0.940
	Precopulatory aggression	20.422	5852.286	<0.001	0.997
	Constant	−11.743	2926.144	<0.001	0.997
Postcopulatory aggression (N=36)	Voracity towards prey	−0.58	0.040	2.120	0.145
	Foraging activity	−0.033	0.030	1.195	0.274
	Male / female weight	−0.480	3.371	0.023	0.887
	Precopulatory aggression	−0.282	1.098	0.067	0.798
	Constant	3.909	2.885	1.835	0.175
Postcopulatory cannibalism (N=36)	Voracity towards prey	−0.002	0.118	<0.001	0.986
	Foraging activity	0.017	0.064	0.073	0.788
	Male / female weight	20.038	7.648	6.864	**0.009**
	Precopulatory aggression	2.813	2.219	1.607	0.205
	Postcopulatory aggression	23.278	9758.555	<0.001	0.998
	Constant	−23.363	4879.284	<0.001	0.997

Significant results are in bold.

above), were performed in SPSS (version 20, IBM Corp., Armonk, NY, U.S.A.).

RESULTS

Behavioural Repeatability

The individual differences in voracity towards prey (quartile variation coefficient: $V = 97.97\%$) were consistent over ontogeny ($R = 0.254$, 95% CI = [0.097, 0.408], $P = 0.001$); and voracity was not affected by females' age, repeat and their interaction (Table 1). Females increased their foraging activity over the subsequent repeats and ages (Table 1). Individual differences in foraging activity (quartile variation coefficient: $V = 100\%$) increased consistently when not taking confounding factors into account (agreement repeatability: $R = 0.307$, 95% CI = [0.013, 0.406], $P = 0.001$). The adjusted repeatability, however, was very low ($R_{adj} = 0.002$, 95% CI = [0.0003−0.0399]).

From 29 females that were subjected to two mating trials (irrespective of whether they mated in the first trial), 55.17%

copulated during the first trial and 27.59% in the second trial. However, fewer females mated or failed to mate in both trials (6.9% and 24.1%, respectively) compared with females that mated either in the first or in the second trial only (48.3% or 20.7%, respectively; link scale repeatability: $R = 0.001$, 95% CI = [0, 0.018]; original scale repeatability: $R = 0.001$, 95% CI = [0, 0.156]).

More than half of the females ($N = 29$) reacted aggressively to courting males, with 52% and 59% in the first and second trial, respectively. However, the consistency over the repeated trials in precopulatory aggression was very low (link scale repeatability: $R = 0.004$, 95% CI = [0, 0.553]; original scale repeatability: $R = 0.003$, 95% CI = [0, 0.471]). The percentage of females that killed the courting male in the first trial (10.3%) doubled in the second trial (20.7%), and precopulatory cannibalism tended to be affected by the interaction of female age∗repeat (Table 1). While 71.4% of females never killed the male during courtship, only one (3.5%) repeatedly cannibalized a male prior to copulation. Between-individual variation in precopulatory cannibalism was too low to assess repeatability.

In the first trial, 11 of 16 females (68.8%) that copulated subsequently attacked the males during or immediately after copulation, although only four attacks resulted in cannibalism. In the second trial, six of eight females that copulated attacked the male (75%), with two attacks resulting in cannibalism. Only one of the 29 females mated and killed her mate in both trials (3.4%). It was not possible to analyse the repeatability of postcopulatory attacks and postcopulatory cannibalism because only two females copulated in both trials.

Behavioural Correlation across Contexts

We found no relationship between the two measures of female aggressiveness in foraging context, i.e. between voracity towards prey and foraging activity (Spearman rho correlation coefficient: $rS = -0.113$, $N = 79$, $P = 0.321$). Aggressiveness towards males during courtship and postcopulatory cannibalism by the females exposed to their first male were significantly related to sexual size dimorphism (Table 2), namely, females were more likely to attack relatively smaller males. Precopulatory aggression, however, did not relate to female voracity towards prey or foraging activity (Table 2). Precopulatory cannibalism and postcopulatory aggression were not significantly related to any of the tested independent variables (Table 2).

Mating Behaviour

In the remating subset of trials ($N = 29$) we found a marginally significant effect of female mating status on mating occurrences (Table 1), where mated females were less likely than unmated females to remate.

Furthermore, we staged mating trials with 76 virgin females, where we repeated trials until either the female mated or the trial was repeated five times. In the first trial, 54% of females mated ($N = 41$). In the second trial we staged matings with females that remained unmated ($N = 32$; three females died) and, of those, 16 females copulated (21.05%). From the remaining unmated females ($N = 16$), one died and six copulated in the third mating trial (7.9%). The fourth trial used eight virgin females (one died); only one female copulated (1.32%), and seven females (9.21%) remained unmated even after the fifth trial.

The Effects on Female Mating Success

Females that remained unmated despite five repeated exposures to males had marginally lower body weight than those females that eventually copulated (Table 3). Mated females did not differ from unmated females in their voracity towards prey (Table 3).

DISCUSSION

Our study of D. fimbriatus failed to provide support for most of the predictions that logically derive from the aggressive spillover hypothesis (Arnqvist & Henriksson, 1997). In particular, we found no evidence for behavioural correlations across contexts: female foraging aggression did not relate to their aggression towards courting males. In contrast, sexual size dimorphism and female mating status explained female aggression towards males during courtship.

Females routinely attacked males during or after copulation, thereby failing to meet the 'interindividual variation criterion' for personality traits (Dingemanse & Dochtermann, 2013; Réale et al., 2007). While we found no correlation between female voracity towards prey and occurrences of postcopulatory attacks and postcopulatory cannibalism during the first mating trial, female success in cannibalizing a male depended on his relative size. In pairs with little difference in size, males were more likely to escape female attacks, as is also the case in other spiders, e.g. D. triton (Johnson, 2005), Hogna helluo (Wilder & Rypstra, 2008), Araneus diadematus (Elgar & Nash, 1988; Roggenbuck, Pekár, & Schneider, 2011).

We failed to find significant (adjusted) repeatability in female foraging activity implying that subsequent repeated tests and age had a larger effect on given measures of foraging activity than 'individuality'. However, the interindividual variation in voracity towards prey persisted over ontogeny, as predicted by the aggressive spillover hypothesis (Arnqvist & Henriksson, 1997) and consistent with the other studies of personality in spiders, e.g. D. triton (Johnson & Sih, 2005); A. studiosus (Pruitt & Riechert, 2009b); Larinioides sclopetarius (Kralj-Fišer & Schneider, 2012); A. pennsylvanica (Berning et al., 2012). However, these studies (Berning et al., 2012; Johnson & Sih, 2005) have not estimated the consistency of individual differences in intersexual aggression levels within the mating context. The repeatability of excessive aggression towards courting males should be costly for females as they risk remaining unmated (Arnqvist & Henriksson, 1997; Elgar & Schneider, 2004). On the other hand, low aggression towards courting males might likewise be costly for the female, for example because of an increase in disease transmission and the energetic costs associated with repeated copulations (Herberstein, Schneider, & Elgar, 2002). Consistent with previous reports (Arnqvist, 1992; Arnqvist & Henriksson, 1997), 50% of virgin females attacked males during courtship in our study, and 10% of males were ultimately killed. However, D. fimbriatus females exhibited no repeatability in aggression towards males during courtship. Instead, they were aggressive in either the first or the second, but rarely showed the same behaviour in both mating trials.

The aggressive spillover hypothesis was initially proposed for D. fimbriatus (Arnqvist & Henriksson, 1997), but we found no

Table 3
The results of logistic regression testing the effects of female body weight and voracity towards prey on their mating success when exposed to up to five males

	B	Bias	SE	P	95% CI	
					Lower	Upper
Voracity towards prey	-0.047	−0.015	0.234	0.162	−0.151	0.027
Female weight	5.605	1.655	5.538	0.064	0.935	22.789
Constant	1.170	0.147	10.932	0.415	−2.904	4.640

$N = 65$. Results are based on 1000 bootstrap samples.

correlation between female voracity in a foraging context and aggression towards males in the mating context. Although our result is intuitive, bearing in mind the costs of excessive aggression for a virgin female (reviewed in Kralj-Fišer et al., 2013), several studies found a correlation between female voracity and precopulatory cannibalism events in other species, e.g. *D. triton* (Johnson & Sih, 2005); *A. studiosus* (Pruitt & Riechert, 2009b); *A. pennsylvanica* (Berning et al., 2012); *Argiope aurantia* (Khadka & Foellmer, 2013); and *Lycosa hispanica* (Rabaneda-Bueno et al., 2014); but see *Nephilingis livida* (Kralj-Fišer et al., 2011). These discrepancies may be explained by either species or methodological differences. For example, the studies may have used different ways in which males were introduced to females (see also Pruitt & Keiser, 2013). Since the most voracious *D. fimbriatus* females in our study instantly attacked any object, whether a fly, a male or a piece of paper when dropped in their close vicinity (personal observations), we introduced a male as far as possible from the female (ca. 40 cm). In this way we allowed the male to court and the female to assess the new stimuli. Most of the males killed prior to mating may therefore be mistaken for prey or, alternatively, be of inferior quality (see above).

The discrepancies across studies may also arise from different approaches to estimating female aggression towards males. We defined all female agonistic behaviours towards males as aggressive behaviours (independently of actual sexual cannibalism occurrences), while most of the above studies measured sexual cannibalism itself. In *L. hispanica* for example, the weight gain was taken as a proxy for female voracity (Rabaneda-Bueno et al., 2014). Kralj-Fišer et al. (2013, p. 620) argued, 'the terms *sexual cannibalism* (effect) and *female aggressiveness* or *tendency to attack and devour males* (cause) should not be used interchangeably as sexual cannibalism is a probable but not the sole consequence of female aggression'. The importance of this distinction is evident in the present study, where female attack success depended on male size and behaviour and not just female behavioural tendencies.

Aggressive spillover predictions ignore the role of male mate choice. However, we found that females with lower body weight were more likely to remain unmated. Those females also received the lowest intensity of male courtship (personal observations). Our result may imply that males choose to copulate with heavier and thus more fecund females (Bondurianskyy, 2001). Male choosiness can be explained by the high risk of postcopulatory sexual cannibalism. In other words, males might prefer to copulate (and be eaten) by fecund females since they offer a potentially higher reproductive output (Buskirk, Frohlich, & Ross, 1984; e.g. Berning et al., 2012; Rabaneda-Bueno et al., 2008; Welke & Schneider, 2012), although this will depend upon the frequency of polyandry and patterns of paternity (Elgar, 1998).

We conclude that cannibalistic species of spiders exhibit consistent individual differences in voracity, which may or may not spill over into aggression towards the male in the first sexual encounter (Berning et al., 2012; Johnson & Sih, 2005; but see this paper), but does not persist over time and does not compromise female reproductive output. Besides female voraciousness, aggression by virgin females towards courting males may be explained by female hunger and male size/weight, whereas postcopulatory cannibalism often depends on mate size dimorphism. The overall results suggest that females are able to adjust their tendency to attack courting males in an adaptive way.

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