

Nutritional implications for sexual cannibalism in a sexually dimorphic orb web spider

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Abstract Models predicting mechanisms driving sexual cannibalism in spiders with sexual size dimorphism (SSD) often assume that spiders use post-copulatory food to channel nutrients into eggs and fecundity is altered through changes in clutch size or egg mass. I tested these assumptions using an orb web spider with extreme SSD, *Argiope keyserlingi*. I fed mated female spiders prey of either high protein-low energy or low protein-high energy composition. I measured egg energy density; a measure of the relative volumes of yolk and albumen. I predicted that if *A. keyserlingi* increase their egg energy density upon feeding on prey of a specific nutrient composition, they could enhance their fecundity by investing in more energy dense eggs. However, if the egg energy densities are dissimilar to their post-copulatory prey they must be drawing energy from their somatic reserves to invest in eggs. In a further experiment I allowed female spiders to mate with and cannibalize males to determine if cannibalism induces similar effects on egg energy density. Male spider protein energy ratio was measured and found to resemble the high protein-low energy prey. I found disagreement between the composition of post-copulatory food and eggs in both experiments. Additionally, spiders fed high protein-low energy prey lost weight indicating that they draw on their energy reserves to invest in eggs. I thus concluded that spiders that feed on high protein-low energy prey or on males increase their egg energy density and, possibly, fecundity. However, the nutrient content of the prey or males cannot provide for investment in eggs. The energy invested in eggs is drawn from somatic reserves, probably induced by an as yet undescribed physiological trigger.

Key words: cannibalism, egg energy density, fecundity, nutrients, orb web spider, sexual size dimorphism.

INTRODUCTION

Reproduction is a key aspect of fitness but comes at a cost. Time, energy and nutrients are invested in courtship, mating and oogenesis often at the expense of somatic growth and defence (Stearns 1992; Wheeler 1996). Sexual cannibalism, where one sex, usually females, consumes another, usually males, is often associated with mating in spiders and mantids (Elgar 1992; Wilder *et al.* 2009). Cannibalism is often employed at times of nutritional stress (Joyner & Gould 1987; Elgar 1992; Mayntz & Toft 2006), so may be a means by which animals attain nutrients not available in allospecific prey. It may thus be supposed that sexual cannibalism provides females with nutrients not otherwise available for investment into eggs (Newman & Elgar 1991; Maxwell 1999; Wilder & Rypstra 2008). However, in the majority of studies on this topic, sexual cannibalism has proved inadequate at providing the female with required nutrients (see reviews by Barry *et al.* 2008 and Wilder *et al.* 2009).

A major nutritional cost for reproducing animals is the nutritional cost of eggs (Vollrath 1987; Jann & Ward 1999). When nutrients are limited, one of two strategies may be employed: (i) produce few nutritionally costly eggs; or (ii) produce many nutritionally inexpensive eggs (Fox & Czesak 2000; McIntyre & Gooding 2000; Mody *et al.* 2007). Eggs are principally composed of lipid (mostly in yolk), protein and water (mostly in albumen) with carbohydrate composition considered negligible (Anderson 1978; McIntyre & Gooding 2000; Booth 2002). Eggs high in yolk lipids are more costly for the female to produce (McIntyre & Gooding 2000; Booth 2002) but reap fecundity benefits as greater yolk investment accelerates embryonic development and ensures that hatchlings emerge fully formed, thus maximizes hatchling survival (Bernardo 1996; Geister *et al.* 2009). Yolk, additionally, may provide food to sustain hatchlings early in post-hatching development and is strongly tied to survivorship beyond the hatchling phase in vertebrates (Bernardo 1996; Radder *et al.* 2004, 2007). It is hence in the female's interest to invest in eggs with as high a volume of yolk as her nutritional environment allows. Egg energy density is a measure of the relative

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proportions of egg yolk and albumen and range from around 17 kJ g⁻¹ (indicating eggs of low yolk: albumen) to around 28 kJ g⁻¹ (indicating eggs of high yolk: albumen) (Anderson 1978; Booth 2002; Riis-Vestergaard 2002). The mean egg energy density of spiders has been measured at 22.6 kJ g⁻¹ (Anderson 1978).

Extreme sexual size dimorphism (SSD; males <25% body weight of females; Barry *et al.* 2008) is a phenomenon most common among orb-web spiders (Orbiculariae). One explanation of SSD in orb web spiders is female gigantism (Kuntner & Coddington 2009) and is based on the idea that fecundity provides selection pressure to maximize female body size (Shine 1988). Most spiders with extreme SSD are sexual cannibals, yet in spiders with extreme SSD sexual cannibalism does not influence fecundity through enhancements in clutch size, egg mass or egg hatching success (Elgar *et al.* 2000; Schneider & Elgar 2001, 2002; Fromhage *et al.* 2003). The conclusions drawn are generally that the small males are inadequate at providing nutrients for females to invest in eggs (Wilder *et al.* 2009; Wilder & Rypstra 2010). This conclusion, nonetheless, is based on a few empirically untested assumptions. One assumption is that the nutrients required for egg investment are drawn directly from any post-copulatory meal. Another assumption is that the only option available to the female for altering fecundity is to invest any acquired nutrients into producing more or larger eggs of similar nutritional quality.

Here I tested these assumptions by conducting experiments where females of the orb web spider *Argiope keyserlingi*, a species with extreme SSD, were fed either high protein-low energy or low protein-high energy food upon mating. I measured the energy densities of *A. keyserlingi* eggs to determine whether egg energy density can be explained by the nutrient content of prey. I also determined the protein: energy ratio of the male spiders to compare them to the experimental prey to investigate whether sexual cannibalism influences *A. keyserlingi* egg energy densities. Any alteration in *A. keyserlingi* egg energy density upon post-copulatory food consumption is indicative of *A. keyserlingi* females influencing their fecundity by altering their relative investment in yolk and albumen. However, only if the energy densities of the prey are congruent with that of the eggs can it be implied that *A. keyserlingi* uses post-copulatory feeding as a means to acquire nutrients to invest in eggs.

METHODS

Spiders and prey

Female *A. keyserlingi* were collected prior to the breeding season (September–October 2006) within the grounds of the

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University of Sydney, Camperdown-Darlington Campus, New South Wales, Australia. I measured the length, carapace width and mass of all of the spiders captured ($n = 102$) and housed them in the laboratory in separate 500 × 500 × 150 mm perspex enclosures. The laboratory was exposed to natural light and the temperature was maintained at 22.0 ± 0.5°C. I acclimated the spiders for 4 weeks, feeding them house flies (*Musca domestica*) twice per week, and fruit flies (*Drosophila melanogaster*) *ad libitum*. Upon acclimation the spiders were re-weighed to ensure only those of similar mass (mass 0.23 ± 0.07 g; $n = 75$ $t = 0.334$; $P > 0.05$) were used in the ensuing experiments. I selected spiders of similar morphology to account for the confounding influence of variability in female aggression.

In flies reared on either standard media supplemented with lecithin-based protein or standard media supplemented with sugar there was a negative correlation between the energy and protein content of the fly tissue according to media (Blamires *et al.* 2009). I thus reared flies from larvae on either of these two media to produce either high protein-low energy flies (reared on high protein media) or low protein-high energy flies (reared on low protein media). Approximately 30 flies were sacrificed by lethal exposure to carbon dioxide, weighed on an electronic balance (CP224, Sartorius, Gottingen, Germany), dried at 60°C for 24 h, re-weighed, ground by mortar and pestle and compressed into 25.0 ± 1.0 mg pellets. The pellets were digested in 5 ml concentrated sulphuric acid at 400°C for 2 h to decompose their proteins and nitrogen content was determined using a Kjeltex direct distillation unit (2300, Trecator, Hoganas, Sweden). Protein concentration was estimated from nitrogen content by a conversion factor (6.25 × % nitrogen). Energy concentrations were determined from protein concentration using the curve of Blamires *et al.* (2009).

Experiments

To determine whether the nutrients in recently fed prey could be incorporated into the nutrients invested in *A. keyserlingi* eggs, wild caught male spiders were introduced into the enclosures of 30 female *A. keyserlingi*. All males were weighed to ensure they were of approximately similar mass (0.03 ± 0.01 g; $n = 30$) and pedipalps examined under a dissecting microscope to ensure only those with pedipalps intact were introduced to females. I prevented cannibalism by removing the males immediately after observing mating and sacrificed them by lethal exposure to carbon dioxide, if not killed by the female. After mating, I fed 15 spiders one high protein-low energy fly every other day until an eggsac was deposited. I fed the other 13 female spiders (two spiders failed to mate) one low protein-high energy fly every other day until an eggsac was deposited. Once an eggsac was deposited the female was reweighed to determine mass gain or loss during the experiment. Prey were anaesthetized using carbon dioxide (to ensure they did not escape from the web), weighed to the nearest mg (to ensure they were of similar mass) and placed in the upper-right corner of the web. Prey carcasses remaining in the web after consumption were removed from the webs and weighed to determine the mass of prey consumed. I removed the eggsacs and opened them using scissors to separate the eggs from eggsacs. The eggs and

eggsacs were weighed and dried (60°C) for 24 h. Upon drying the eggs and eggsacs were re-weighed, ground using a mortar and pestle, and compressed into 25.0 ± 1.0 mg pellets and egg energy density measured using a micro-bomb calorimeter (Gentry, Aiken, SC, USA). I separated eggs and eggsacs for nutritional analysis as the eggsac is comprised principally of silk, thus high protein, so including it with the eggs would give an underestimation of egg energy density.

To determine whether it is likely that *A. keyserlingi* incorporates the nutrients of consumed males into eggs, I introduced virgin wild caught adult males (mass = 0.02 ± 0.01 g; $n = 45$) into the enclosure of laboratory acclimated females (mass = 0.24 ± 0.1 g; $n = 45$). Once a male was introduced the feeding was reduced to one to two flies per week. All enclosures were constantly monitored for mating and cannibalism between 0800 and 1900 h over 1 week. I noted which females cannibalized their partner upon mating ($n = 29$); removing any males that mated without being cannibalized ($n = 16$). I did not assess the aggressiveness of individual females to determine if aggression influences cannibalism or egg energy investment. Nevertheless, as cannibalism was interrupted, and food intake and female morphology controlled in the previous experiment, any influence of female aggression should show in that procedure. Each eggsac ($n = 27$ from cannibalistic spiders and $n = 15$ from non-cannibalistic spiders; $n = 3$ did not deposit an eggsac) was removed from the enclosure upon deposition and opened and eggs removed. All females were reweighed upon eggsac deposition to determine the mass gain or loss during the experiment. The clutch was counted under a dissecting microscope. The eggs and eggsacs were separately weighed, on an electronic balance and dried (60°C) for 24 h. Upon drying the eggs and eggsacs were re-weighed, ground using a mortar and pestle, and compressed into 25.0 ± 1.0 mg pellets and egg energy density measured using a micro-bomb calorimeter. All males removed from webs in the previous experiment and an additional 10 males taken from the field were dried, weighed, crushed and compressed to determine protein concentration for comparison with the high protein-low energy and high energy-low protein flies.

Statistical procedures

I used paired *t*-tests to compare the pre- and post-experimentation masses of females between treatments. I

compared the egg energy densities of cannibalistic and non-cannibalistic female *A. keyserlingi* by one-factor (presence or absence of cannibalism) analyses of variances (ANOVAs). The amount of prey consumed and frequency of consumption by spiders differs with prey nutrient constituency (Mayntz *et al.* 2005, 2009; Blamires *et al.* 2009). I therefore compared the egg energy density of female *A. keyserlingi* fed high protein and low protein prey by a series of one-factor (prey type: high protein or low protein flies) analyses of covariance (ANCOVAs). The mass of prey consumed (prey mass minus carcass mass) was the covariate used. I also compared clutch size, clutch mass and eggsac energy density across treatments by ANOVA/ANCOVA to determine if *A. keyserlingi* compensates for changes in egg energy density by altering any of these parameters. I conducted Kolmogorov-Smirnov and Levene's tests to test the normality of distributions and homogeneity of variances, respectively, before conducting analyses. Data that failed these tests were log-transformed. I used Parallelism tests to ensure slopes were parallel before conducting ANCOVA. I used Tukey's Honest Significant Difference analyses to determine the differing means when significance was detected. Bonferroni corrections (Rice 1989) were applied where appropriate to account for the multiple testing.

RESULTS

The high protein-low energy and low protein-high energy flies differed significantly in protein content (high protein-low energy flies = $66.94 \pm 4.27\%$ protein, energy density = 23.41 kJ g^{-1} , low protein-high energy flies = $43.55 \pm 5.35\%$ protein, energy density = 24.82 kJ g^{-1}) although the dry mass consumed of each of the types of fly was similar between treatments (Table 1). Spiders fed high protein-low energy flies produced eggs of greater energy density than those fed the low protein-high energy flies ($26.51 \pm 3.54 \text{ kJ g}^{-1}$ compared with $21.83 \pm 1.72 \text{ kJ g}^{-1}$) (Fig. 1). Upon completion of the experiment the high protein-low energy fed spiders (mass = 0.10 ± 0.02 g) weighed significantly less ($t = -0.573$; $P < 0.001$) than the low protein-high energy fed spiders (0.18 ± 0.06 g). These results

Table 1. Results of one-factor ANCOVAs (d.f. = 1,13) comparing dry mass and protein concentration of high protein-low energy flies, low protein-high energy flies and male *Argiope keyserlingi*, and the influence (ANCOVA, d.f. = 2,12) of feeding on high protein versus low protein flies on: clutch size, clutch mass, eggsac mass, egg energy and eggsac energy

	High protein-low energy flies	Low protein-high energy flies	Male spiders	F-statistic	P
<i>n</i>	15	13	6		
Dry mass (g)	0.211 ± 0.06	0.206 ± 0.05	0.022 ± 0.01		
% protein	66.94 ± 4.27^a	43.55 ± 5.35^b	59.98 ± 4.21^a	59.234	<0.0001
Clutch size	247.76 ± 60.82	231.70 ± 41.12		2.205	0.402
Clutch mass (g)	0.60 ± 0.03	0.56 ± 0.02		0.291	0.483
Eggsac mass(g)	0.18 ± 0.06	0.23 ± 0.11		2.816	0.067
Egg energy (kJ g^{-1})	21.83 ± 1.72	26.51 ± 3.54		7.563	0.046 [†]
Eggsac energy (kJ g^{-1})	22.67 ± 1.92	21.44 ± 0.56		1.262	0.598

[†]Insignificant after Bonferroni correction. Tukey's Honest Significant Difference: a > b.

indicate that *A. keyserlingi* eggs are nutritionally dissimilar to the prey consumed post-copulation and that they draw on energy reserves, not recently eaten food, to invest in eggs. Clutch size, clutch mass, eggsac mass and eggsac energy were not significantly different between spiders fed high protein-low energy flies and spiders fed low protein-high energy flies (Table 1), hence these parameters are not altered to counter the investment in egg energy density.

Argiope keyserlingi that cannibalized males produced eggs with greater energy density than spiders not engaging in cannibalism (egg energy density of cannibal spiders = $25.35 \pm 3.71 \text{ kJ g}^{-1}$; non-cannibal spiders = $21.62 \pm 2.14 \text{ kJ g}^{-1}$; Fig. 1). Clutch size, clutch mass, eggsac mass and eggsac energy, nonetheless, were unaffected by cannibalism (Table 2). This suggests that *A. keyserlingi* that consume males post-copulation may influence their fecundity without adjusting egg mass or clutch size. Upon completion of this experiment the non-cannibal spiders (mass =

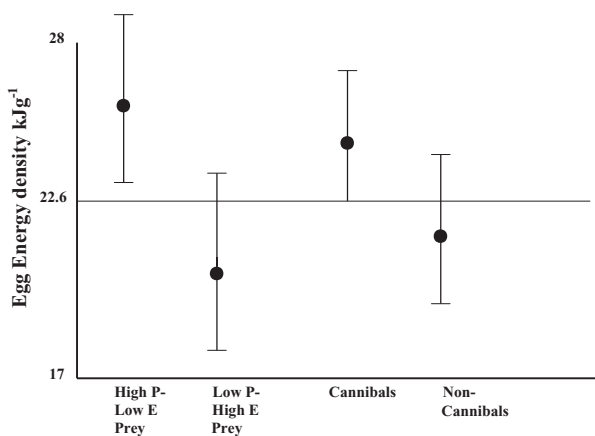


Fig. 1. The energy density of *A. keyserlingi* eggs upon post-copulatory feeding on either: high protein-low energy prey, low energy-high protein prey, conspecific males (cannibals) or nothing (non-cannibals). The estimated mean egg energy density for spider eggs (22.6 kJ g^{-1} ; Anderson 1978) is indicated.

Table 2. Results of one-factor ANOVAS (d.f. = 1,15) comparing: clutch size, clutch mass, eggsac mass, egg energy and eggsac energy, between female *A. keyserlingi* that consumed males (cannibals) and those that did not consume males (non-cannibals)

	Cannibals	Non-cannibals	F-statistics	P
n	27	15		
Clutch size	226.54 ± 27.84	225.13 ± 47.26	0.383	0.439
Clutch mass (g)	0.58 ± 0.01	0.56 ± 0.06	0.571	0.502
Eggsac mass(g)	0.19 ± 0.06	0.22 ± 0.11	1.171	0.208
Egg energy (kJ g^{-1})	25.35 ± 3.71	21.62 ± 2.14	6.510	<0.001
Eggsac energy (kJ g^{-1})	21.43 ± 0.96	20.24 ± 1.56	0.517	0.488

$0.10 \pm 0.09 \text{ g}$) weighed significantly less ($t = -6.08$; $P < 0.01$) than the cannibal spiders ($0.16 \pm 0.07 \text{ g}$). The protein concentration of male spiders ($59.98 \pm 4.21\%$, energy density = $23.98 \pm 2.58 \text{ kJ g}^{-1}$) was not significantly different from the protein concentration of the high protein-low energy flies but was significantly different from that of the low protein-high energy flies (Table 1). Post-copulation consumption of male spiders, as with the high protein-low energy flies, thus cannot explain the enhanced energy investment in eggs in spiders engaging in cannibalism.

DISCUSSION

In this study I found that feeding on both high protein-low energy prey and conspecific males induced *A. keyserlingi* to produce eggs with higher egg energy densities. As egg energy density is an indicator of yolk density and yolk is implicit in more rapid development and survivorship beyond the egg, feeding on high protein prey and/or males may serve to enhance fecundity in *A. keyserlingi*. I also found that the energy density of *A. keyserlingi* eggs was dissimilar to that of both the high protein-low energy prey and conspecific males so the implied fecundity enhancement cannot be ascribed to the females channelling nutrients from these prey into their eggs. This study agreed with previous studies stating that the males in spiders with SSD are too small (*A. keyserlingi* males being <10% the body weight of females) to provide nutrients for direct investment in eggs (Elgar *et al.* 2000; Schneider & Elgar 2001, 2002; Fromhage *et al.* 2003) so the energy invested in eggs by *A. keyserlingi* must come from somatic energy reserves. This would explain why female spiders investing in greater egg energy lost weight.

The increased egg energy investment in spiders that cannibalized males suggested that a fecundity advantage may be bestowed to *A. keyserlingi* cannibals by mechanisms other than nutrient extraction from its prey. Schneider and Elgar (2002) found that aggressive *Nephila plumipes* females tend to engage in cannibalism more, grow faster and produce more eggs than less aggressive females. They interpreted these findings as

aggressive spiders physiologically utilizing nutrients differently. Aggressive *A. keyserlingi* females could have invested more heavily in egg lipids than non-aggressive females in my study. I would have nonetheless expected less decisive differences in egg energy densities between treatments in the first experiment had aggression alone influenced egg energy investment. As I selected females of similar morphology, it was unlikely that any overtly aggressive or overtly submissive females were used in my experiments. Schneider and Elgar did not specifically examine nutrient use in aggressive and submissive *N. plumipes* so it may be possible that aggressive and non-aggressive spiders metabolize and allocate nutrients similarly but still invest in eggs of higher energy density. Further studies using multiple taxa may shed light on how aggressiveness in different spiders influences their nutrient use and ability to physiologically alter fecundity. Aged females may also deposit more yolk into their eggs than younger females (McIntyre & Gooding 2000) and, coincidentally, engage more often in cannibalism; perhaps because their hardened cuticle is or more difficult for the male to penetrate and the opportunities for cannibalism are increased (Sasaki & Iwahashi 1995; Schneider & Elgar 2002; Foellmer & Fairbairn 2004). As I collected only sub-adult females and used those of approximately equal size, it is unlikely that age or prior mating experience influenced the mating strategy or yolk investment by the females in my experiments. Female age and/or aggression therefore is unlikely, although cannot be entirely ruled out, as an explanation for the patterns in egg energy investment found in spiders feeding on high protein-low energy prey and spiders engaging in sexual cannibalism.

Models explaining why spiders with SSD do not attain nutrients for eggs via consumption of males are based on the optimal foraging model which states that animals that consume more prey gain more energy to invest in reproductive effort (Stephens & Krebs 1986). This model, however, has been modified to include nutrients such as protein, lipids, salts and vitamins as currencies (Slansky & Rodriguez 1987; Guglielmo *et al.* 1996; Simpson *et al.* 2004, 2006; Mayntz *et al.* 2005). Mayntz *et al.* (2005) suggested that spiders forage to balance their protein to fat intake ratio. Protein has also been suggested as being an important provider of amino acids for web building (Craig 2003; Blamires *et al.* 2009; Mayntz *et al.* 2009). I found that when *A. keyserlingi* females fed on both high protein-low energy prey and the high protein male spiders they produced egg of greater energy density. Moreover, the egg energy densities of spiders feeding on high protein-low energy prey and male spiders was considerably higher than has been reported for most other spiders (Anderson 1978). This may be indicative that protein is needed by reproductive females in order to draw energy from their somatic reserves to invest in egg

yolk. Perhaps a physiological trigger is initiated when feeding on protein concentrated prey. Future studies may uncover whether such a trigger exists and, if so, its source and actions.

In summary, I found that feeding on high protein-low energy prey and/or males induces female *A. keyserlingi* to produce eggs of greater egg energy density. As egg energy density is indicative of yolk investment consuming high protein post-copulatory food may indirectly bestow *A. keyserlingi* greater fecundity. As the males are considerably smaller than the females and the nutrient composition of both the high protein-low energy flies and male spiders are dissimilar to that of the eggs, it is not possible that post-copulatory feeding on these prey enables *A. keyserlingi* to extract the nutrients needed to increase their egg energy densities. Rather, *A. keyserlingi* draws the energy needed for its eggs from somatic reserves. The trigger for releasing the stored energy is unknown but appears to be related to protein uptake. There are various models that explain why there is much diversity in the incidence of sexual cannibalism among spiders, even among closely related species. These models generally rule out nutrient uptake in species with extreme SSD. My study, however, suggested some of the assumptions upon which the models are based need revising. A comparative study of the cannibalistic tendencies in spiders using species with varying degrees of SSD, in conjunction with a comparative study of nutritional physiology, may shed more light on the relative influence of nutrients, SSD, innate aggression and other such behavioural syndromes (Johnson & Sih 2005) in driving cannibalism in spiders.

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