

HOW FEMALE DIET IMPACTS LIFE HISTORY
TRAITS IN THE TRIANGULATE COBWEB SPIDER:
EFFECTS OF NUTRITION ON FEMALES AND THEIR
OFFSPRING

By

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Abstract: In spiders, nutrients in a mother's diet are provided to her offspring through the eggs she produces, and consequently food quality may impact offspring life history traits. In this study, I tested the effect of maternal diet quality on egg sac production and offspring survival in *Steatoda triangulosa*, the triangulate cobweb spider. The nutritional quality of a female's diet was experimentally manipulated by feeding her fruit flies with a gradient of lipid and protein. I measured several life history traits both for the female and her offspring, including female body size at maturation, number of egg sacs produced, whether or not those egg sacs were viable, and offspring quality. I evaluated two main predictions. First, that females fed the high protein diet would produce more egg sacs than females fed the low protein (high lipid) diet. Second, that offspring whose mothers were reared on the high protein diet would have higher survival rates and would develop faster than those offspring whose mothers were reared on the low protein diet treatment. Results showed that the female spider's diet had a large impact on her reproductive success. Of the 94 females in the study, 22 produced egg sacs, with 11 of these producing multiple egg sacs. Females in the protein treatments were more likely to produce an egg sac (viable or not) and a higher average number of egg sacs per female, than in other treatments. Only females fed a protein-enriched diet made viable egg sacs that ultimately produced surviving spiderlings. The high protein mother's spiderlings had a higher survival rate through the first and final molt and also developed at a faster pace than the intermediate protein mother's spiderlings.

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CHAPTER I

HOW FEMALE DIET IMPACTS LIFE HISTORY TRAITS IN THE TRIANGULATE COBWEB SPIDER: EFFECTS OF NUTRITION ON FEMALES AND THEIR OFFSPRING

Introduction

Maternal effects, including a mother's experience in the environment, can lead to variation in her development and condition that can be passed on to her offspring and influence their growth and survival (Mousseau & Dingle 1991; Mousseau & Fox 1998; Wilder 2013). Since most arthropods do not provide a lot of direct parental care, indirect maternal effects may be very important, way that parents influence offspring success in variable environments. Nutrition is one important factor that could influence maternal effects. It's been shown that the nutrient content of the mother's food is provided to her offspring through the eggs she produces and has shown to impact offspring life history traits (Tallamy & Wood 1986; Mousseau & Fox 1998). Differential provisioning of offspring can have significant consequences to offspring fitness (Benton et al., 2005). In some species, the mother can determine the amount and quality of resources to allot to the eggs during egg laying, resources that have a large influence on such characteristics as survival, growth, and reproductive success of the offspring (Mousseau & Fox 1998). Those eggs provisioned with higher quality food usually have higher survival rates, growth rates, probability of developing into larger adults (Tallamy & Wood 1986;

Gonzaga & Leiner 2013).

In addition to diet quantity, recent work has shown that the nutrient content of food (i.e., diet quality) can have important impacts on growth and reproduction. Previous studies of how nutrients impact life history traits of spiders have examined the outcomes of directly manipulating spider diets (Table 1). For example, Taylor & Pfannenstiel (2009) studied the importance of nectar as a food supplement for the spider *Cheiracanthium inclusum*. Spiderlings of this species were reared on eggs of *Helicoverpa zea* with treatments split into those with nectar added or nectar not added (Taylor & Pfannenstiel 2009). They found that adding nectar to prey increased spiderling lifespan and the number of molts, and almost all of the spiderlings became adults. In contrast, spiderlings reared without the nectar supplement never matured to adulthood (Taylor & Pfannenstiel 2009). Females reared on prey with added nectar also had higher fecundity (Taylor & Pfannenstiel 2009). Another study examined the effect of diet on instar duration and growth in two species of juvenile wolf spiders, *Pardosa prativaga* and *Pardosa amentata* by manipulating dietary nutrients for six treatments of *Drosophila melanogaster* that were given a range of protein and lipid content (Jensen et al. 2011b). Those spiders fed prey with higher protein content had both higher growth rates and larger carapaces, especially in *P. amentata* (Jensen et al. 2011).

Bilde & Toft (2001) looked at the value of three different aphid species as prey for the linyphiid spider, *Erigone atra*. The spiders were split up into eight diets: three single-species aphid diets, a mixed diet of all three aphid species, three mixed diets with each aphid species grouped with *Drosophila melanogaster*, and a high quality comparison diet made up entirely of *D. melanogaster* (Bilde & Toft 2001). The media

that the fruit flies were raised on included a supplement of crushed dog food, which provides a high percentage of protein, fat, and many vitamins and minerals (Mayntz & Toft 2001). They found that spiders in the fruit fly diet groups produced significantly more eggs than those in the aphid-only diet groups (Bilde & Toft 2001). Also, compared to the fruit fly diet groups there was a fast decline in egg sac and egg production in the single-species and mixed-aphid diet groups (Bilde & Toft 2001).

Few studies to date have explicitly examined the diet of the mother and how that affects the life history traits of her offspring. One such study of the subsocial spider, *Stegodyphus lineatusone*, found that those female spiders that were raised on a protein-enriched diet had an increase in body size compared to mothers in other diets (Salomon et al. 2011). Despite the role of protein in egg production, no effect was found with regard to maternal diet on the number and mass of eggs produced while the mother was on the diet from maturation until oviposition (Salomon et al. 2011). Mothers on the protein-enriched diet had higher offspring survival than mothers on either intermediate diet, but this occurred when the mother was placed on the diet after oviposition until matrophagy took place and she was eaten by her offspring (Salomon et al. 2011).

Several studies above manipulated a diet in a broad way that included a high quality and low quality diet type but were unclear how these diets differed in quality. Recent work has started to focus more on the impacts of specific macronutrients in prey (i.e. lipid and protein) and how these diets can affect the growth and development in spiders (Jensen et al. 2011a,b; Wilder 2011; Wilder 2013). Of those studies that have found that high quality prey affects the predator, the prey was rich in protein (Mayntz & Toft 2001; Jensen et al. 2011a; Salomon et al. 2011; Jensen et al. 2012). This suggests

that a predator's high growth rates may be limited by protein intake as well as by energy (Mayntz & Toft 2001; Jensen et al. 2011a; Jensen et al. 2012). Spiders use protein for building protein-rich eggs, development, and for energy (Wilder 2011; Barry & Wilder 2013). Silk production also depends on protein. For example, female *Argiope keyserlingi* had longer silk decorations in their webs when they were provided prey with a high-protein content compared to prey with a high-lipid content (Blamires et al. 2009; Wilder 2011). Because amino acids are a key component of spider silk, prey protein content had a large effect on web building in this species (Foelix 1996; Wilder 2011). Nevertheless, high energy lipids can be used in egg production and investment, plus providing energy to fuel daily metabolic costs (Wilder 2011).

The goal of this study was to test the effect of maternal diet quality on egg sac production and offspring survival and development in *Steatoda triangulosa* (the triangulate cobweb spider) (Walckenaer 1802). Based on previous studies, I predicted that females fed a high protein diet will produce more egg sacs with more of them being viable than females fed a low protein (high lipid) diet. I also predicted that offspring whose mother is reared on the higher protein diets will have higher survival and will develop faster than those offspring whose mother is reared on the lower protein (higher lipid) diet.

An important component of this study was teasing apart the impact of specific macronutrients within the prey and their effects on spider life history traits. By examining the role of nutritional quality on reproductive success of adult females and offspring life history traits in this species, I hope to provide insight into how nutritional deficiencies

can affect both mothers and their offspring and have consequences on ecologically relevant scales.

METHODS

Study species: The triangulate cobweb spider (*Steatoda triangulosa*) is a common house spider in the family Theridiidae. Adult spiders are approximately 3.5 to 5.5 mm long (females 4–5.2 mm, males 3.5–4 mm) (Kaston 1948). Found in many parts of the world, *S. triangulosa* originated in Eurasia, was introduced to North America during European colonization and is now widespread (Levi 1962; Draney 2001). Triangulate cobweb spiders are comb-footed spiders that construct irregular tangle webs (Benjamin & Zschokke 2002) in which they catch an array of prey, including a variety of insects and arachnids as well as isopods (Levy & Amitai 1982). In preliminary work raising these spiders in the lab, the number of spiderlings in an egg sac ranged from 3-150 and maturity was reached after three molts for males and four molts for females. Time between producing egg sacs can range from 3-50 days. Mating occurs between May and October and females can produce anywhere from 1-10 egg sacs during a season (Kaston 1948).

All experimental spiders were raised in the lab from the egg sacs of wild-caught females collected in April-June 2015 from garages, basements, and outbuildings in various locations around Stillwater, Oklahoma. Individuals were housed in separate, translucent, 16-oz plastic containers at a temperature of 21.2-23.2°C and a diurnal period of 12 light hours per day. Wild-caught females were fed mealworms once a week and allowed to produce egg sacs, with eggs fertilized by sperm stored prior to capture. Ten

spiderlings per egg sac were selected at random and housed individually in 1-oz containers (n=41 egg sacs, n=410 spiderlings). Developing spiderlings were fed *Drosophila melanogaster* once a week until assigned to a diet treatment sixty days after their fourth molt.

The prey species, *Drosophila melanogaster*, is commonly used for diet manipulations. I manipulated *D. melanogaster* body nutrient content by supplementing fly media with either casein powder or sugar in various amounts (Mayntz et al. 2005; Jensen et al. 2010). Flies were fed one of five diets with varying ratios of lipid and protein content (Table 2): *Lipid-rich* flies were raised on a 1:2 ratio of sucrose and basic medium; *intermediate lipid* flies were raised on a 1:4 ratio of sucrose and basic medium; *standard* flies were raised on basic medium; *intermediate protein* flies were raised on a 1:4 ratio of casein and basic medium; and *protein-rich* flies were raised on a 3:2 ratio of casein and basic medium (Jensen 2010; Jensen 2011a; Wilder 2011). Fruit fly diet was found to impact their body composition (see results). From this initial population of lab-raised spiderlings, 100 females were randomly assigned to one of five feeding treatments. By the end of the study, there was a small decrease in the total sample sizes: high lipid (n=17), intermediate-lipid (n=19), no supplement (n=19), intermediate-protein (n=19), and high-protein (n=20). The six females that died during the study were fairly evenly distributed across treatment groups and not included in analyses. To give the female cobweb spiders ample time to incorporate the nutrients from the flies and pass those nutrients to their offspring, treatments lasted for 150 days.

Two weeks after starting the diet treatment, each female was paired with a lab-raised, unrelated male and was observed to mate at least one time before being separated

(n=94 males). Although I expected females to initiate egg sac production shortly after mating, only a few females did so. Therefore, I decided to move each female to a larger container (2-oz) with a bent piece of cardboard added to provide cover for the female. This was done for all study females ninety days after beginning the treatment.

Each female was observed daily to record egg sac production, total number of egg sacs and egg sac viability. Once spiderlings hatched from an egg sac, I counted the total number of offspring per egg sac, and measured the survival rate, sex, and development of each spiderling. I used carapace width and the combined length of the tibia and patella, to the nearest 0.01 mm, as a measure of spider size (Jakob et al. 1996; Wilder 2013). Infinity Analyze software was used for image capture and measurement.

Body content analysis of female spiders and fruit flies

At the end of the experiment, all female spiders and thirty female flies (as one sample) from each treatment were sacrificed by freezing. The protein and lipid content analysis for the flies was performed three separate times and the average of the three results was taken. To assess both the nutrient content of the fruit flies as well as the nutrient content of the female bodies at the end of the study, I used a chloroform extraction to measure the lipid content and a Bradford Assay for the protein content (Wilder & Rypstra 2010; Jensen et al. 2011; Schmidt et al. 2012). For the lipid analysis, each sample was dried at 60°C for 24-h and then weighed. Lipids were extracted in two 24-h washes of chloroform, and samples were again dried and weighed (Wilder & Rypstra 2010; Jensen et al. 2011; Schmidt et al. 2012). The mass of lipid present in the spider and diet flies was calculated as the difference in mass before and after chloroform

extraction (Wilder & Rypstra 2010; Jensen et al. 2011). Protein was measured using 3-6 mg of ground lean tissue from each sample. A combination of NaOH, sonication, and heat (90°C) was used to extract soluble protein from the tissue (Barry & Wilder 2012; Schmidt et al. 2012). The samples were centrifuged and undigested tissue was formed into a pellet, which was then removed and analysis was conducted on the supernatant (Barry & Wilder 2012; Schmidt et al. 2012). This colorimetric protein assay is based on an absorbance shift of dye Coomassie Brilliant Blue G-250. Samples were read at 595 nm using a spectrophotometer (Schmidt et al. 2012). The elevated absorbance at this wavelength reflects increased binding of protein bonds to Coomassie dye, therefore the higher the value at this wavelength, the higher the amino acid content in the sample. I analyzed each sample in triplicate and each plate had its own standard curve, using IgG as a protein standard (Barry & Wilder 2012; Schmidt et al. 2012). The weights of each were used to calculate the percent lipid, percent protein and the ratio of lipid to protein for each sample (Schmidt et al. 2012).

Spiderling development

All spiderlings that emerged from the egg sacs were fed twice weekly on *D. melanogaster* reared on fly media with no supplement added. Developmental data included survival through the first and final molt, sex of each spiderling, and the date each spiderling molted to track its development.

Statistical Analysis of egg sac production

The overarching approach I used to analyze my data was model comparison (Anderson 2008; Burnham & Anderson 2013). This approach was used to evaluate the

plausibility of competing models or hypotheses (Franklin et al. 2001; Symonds & Moussalli 2011; Burnham & Anderson 2013). As an alternative to null hypothesis testing, this method is used widely by ecologists, behavioral biologists, and conservationists (Burnham et al. 2011; Richards et al. 2011; Symonds & Moussalli 2011). Although not as common, a number of empirical studies on spiders are now also employing this approach (Buzatto et al. 2007; Pruitt & Reichert 2011; Unglaub et al. 2013; Chiavazzo et al. 2015; Stoffer & Uetz 2015).

All data analysis were conducted using the R statistical package (R Core Team 2015, version 3.2.3). For data visualization, boxplots were used. A boxplot is a standardized way of displaying the distribution of data and includes values for the data minimum, first quartile, median, third quartile, and maximum. To analyze egg sac production, I used generalized linear models (GLMs) with a binomial and Poisson link. The link function is used within GLMs to indicate that the response variable is modeled by a probability distribution from the exponential family (e.g., binomial and Poisson). GLMs use maximum likelihood to estimate parameters of statistical models. To measure the relative performance of the models according to information criteria (specifically AICc), I used the R package MuMIn (Wagenmakers & Farrell 2004; Symonds & Moussalli 2011; Burnham & Anderson 2013; Barton 2016). AICc is a numerical value assigned to rank competing models in terms of information loss and how well the model fits the data. The model with the lowest AICc is the ‘best approximating model’ (Symonds & Moussalli 2011) of the response variable.

Sixty-four models were constructed that included combinations of morphological measurements, whether or not a female produced an egg sac, total egg sac number per

female, viable egg sac production, and treatment. The female's morphological variables (body weight & tibia length) were included in the full model as potential predictors, with the model comparison approach used to determine their relative importance. Tibia length is typically used as a measure of body size for web-building spiders, therefore, carapace width was excluded from the analysis (Jakob et al. 1996; Wilder 2013). Carapace width and tibia length are highly correlated (0.827). Tibia length is a more accurate measurement of body size for web-building spiders so we chose this variable over carapace width. These models were analyzed using model selection based on Akaike information criterion (AIC) model selection approach to determine which treatment type best explained the production of egg sacs and performance in spiderlings (Burnham & Anderson 2011; Symonds & Moussalli 2011; Burnham & Anderson 2013). Using the $\Delta AICc$ scores and AICc weights, I identified the top candidate models by removing models with $\Delta AICc$ scores greater than 6. I used general linearized models and compared a set number of models to a data set and measured the relative support the data gave to each model (Burnham & Anderson 2011; Symonds & Moussalli 2011; Burnham & Anderson 2013). Among a set of alternative models, the Akaike weight is the relative likelihood that a given model is the best model describing the data (Symonds & Moussalli 2011). The relative variable importance is the sum of 'Akaike weights' over all models including the explanatory variable (Barton 2016).

Statistical Analysis of spiderling development and size

Using generalized linear models I produced similar models containing the morphological traits of the spiderlings. I then performed the same AIC models selection approach previously mentioned. Again removing models with $\Delta AICc$ scores greater than

6. I used the lme4 package (Bates et al. 2015) in R to build mixed-effects models to examine the random effect of the egg sac along with treatment on offspring survival and development. Mixed-effects are useful when the data contain correlated structures (Zuur et al. 2009). Correlations arise from grouped data, which occurs when data are collected in a hierarchical structure, such as when observational units are related (Zuur et al. 2009). Spiderlings from the same egg sac have both a shared environment and are related, such that each spiderling is not truly independent, so egg sac was added to the model as a random effect.

RESULTS

Fruit fly body content

Flies raised on sugar-rich media contained more lipids and less protein compared to female flies raised on protein supplemented media (Figure 1), confirmation that our dietary treatment groups were correctly implemented and represented a gradient in lipid:protein content of prey provided to females.

Whether or not a female produced an egg sac

Of the 94 total female spiders pooled among diet treatments, 22 females (23.4%) produced egg sacs. The best supported model for whether or not a female produced an egg sac included treatment, tibia length, and the age of the female (GLM with a binomial link; Tables 3 and 4). Treatment had a negative impact on whether or not a female produced an egg sac, meaning that those female spiders with the lowest treatment ratio (the protein treatments) were more likely to produce an egg sac compared to those spiders with the highest treatment ratio (the lipid treatments) (Figure 2). Treatment was included

in 8 out of the 15 candidate models and had the highest relative importance (0.95) out of any variable (Table 4).

Time to first egg sac

Figure 3 shows survival curves for number of days to first egg sac by treatment. Across time, a higher proportion of females in the lipid treatments remained without an egg sac, while more females in the protein treatments made their first egg sac. In all five treatments, there were female spiders that had yet to produce an egg sac by 150 days (the end of treatment) (Figure 3). In survival models of days to first egg sac production, treatment was included in 8 out of the 8 candidate models and had the highest relative importance out of any variable (0.93) (Table 5).

Egg sac production

A boxplot shows that females tended to produce more egg sacs in the protein treatments compared to the lipid treatments (Figure 4). The best supported model for analyzing egg sac production included treatment, tibia length, and age of the mother (GLM with a Poisson link; Table 6). Treatment had a negative impact on egg sac production—in other words, those female spiders with the lowest treatment ratio (the protein treatments) were more likely to produce egg sacs compared to those spiders with the highest treatment ratio (the lipid treatments). Treatment had the highest importance (1.00) and was included in 8 out of the top 15 candidate models (Table 6). As a group, female spiders on the protein treatment produced 38 egg sacs, while the lipid treatment females produced only 9 egg sacs.

Viable egg sac production

The best supported model for whether or not a female produced a viable egg sac included treatment, age, and initial weight of the female (GLM with a binomial link; Table 7). Again, treatment had a high relative importance (0.87) and was included in 8 out of the 15 candidate models (Table 7). In addition, females that were in the treatments with the lowest lipid: protein ratios (the protein treatments) on average produced a higher number of viable egg sacs than any other treatment (treatment again had a negative impact). There were no viable egg sacs produced in the lipid treatments. Six females produced fifteen viable egg sacs in protein treatments and one female from the standard media treatment produced one viable egg sac.

Number of spiderlings hatched

The best supported model for number of spiderlings hatched from each viable egg sac included treatment, age, and size of the female (GLM with a Poisson link; Table 8). Treatment had a high relative importance (1.00) and was included in 8 out of the 15 candidate models (Table 8). There were more spiderlings produced per female in the high protein treatment compared to the intermediate protein treatment and standard treatment (Figure 5). The total number of hatched spiderlings was greatest in the high protein treatment (n=102), with the smallest number of hatched spiderlings coming from the one viable egg sac produced in the standard treatment (n=6). There were no viable egg sacs, and thus no spiderlings, produced by female spiders in the lipid treatments.

Protein & Lipid content of females

If female spiders simply retained the nutrients in the same ratio that they were fed, one would predict a positive correlation of treatment ratio with post-trial lipid mass, and a

negative correlation of treatment ratio with post-trial protein mass. Looking at the post-trial lipid and protein mass of each spider, I found that female spiders in the lipid treatments finished with a higher post-trial lipid mass than those females in the protein treatments (correlation coefficient = 0.559) (Figure 6a). However, females in the protein treatments finished with a lower post-trial protein mass than females in the lipid treatments (correlation coefficient = 0.190) (Figure 6b). In other words, a positive correlation, not negative, was found between treatment ratio and post-trial protein mass. This suggests that protein-enriched females lost or used the protein from their food source, quite plausibly in the production of egg sacs. Figure 7 shows the distribution of females' post-trial protein mass across treatments. The median of the post-trial protein mass of females who produced two or more egg sacs was lower than the median for the post-trial protein mass of females who produced 0-1 egg sac (Figure 7).

Long-term impacts on offspring

For spiderling results, the analysis focused on intermediate and high protein treatments and excluded the standard treatment mother's spiderlings due to the small sample size and low survival rate. (Of the six spiderlings that hatched from the standard treatment's egg sac, only one survived through the first molt, and no spiderlings survived through the second molt.) Lipid treatments are also excluded because there were no spiderlings produced in these treatments.

Of the spiderlings produced by mothers in the intermediate protein treatment, 75% survived through their 1st molt (n=68 of 90) compared to 89% in the high protein treatment (n=91 of 102). Looking at individual mothers, a higher number of spiderlings

survived in the high protein treatment compared to the intermediate protein treatment (Figure 8a and b). In the mixed-effects model, treatment was not a significant coefficient when egg sac was treated as a random effect ($z = 1.706, P = 0.09$), although the trend is in the same direction (Table 9). Of those spiderlings that survived through the 1st molt, the number of days it took them to go through their 1st molt differed between treatments, with spiderlings from high protein mothers reaching the 1st molt in fewer days than the spiderlings from intermediate protein mothers (Figure 9). However, mother's diet treatment was not a significant coefficient when egg sac was treated as a random effect in survival analysis ($z = 0.63, P = 0.53$) (Table 10).

Of the spiderlings produced by mothers in the intermediate protein treatment, 49% survived through their 3rd molt (n=46 of 90) compared to 81% in the high protein treatment (n=19 of 102). In this case, treatment was a significant coefficient when egg sac was treated as a random effect in the mixed-effects models ($z = 2.824, P < 0.005$) (Table 11). Of those who survived, spiderlings of high protein mothers reached their 3rd molt in fewer days than spiderlings of intermediate protein mothers (Figure 10) (intermediate protein: $\bar{x} = 73.3, SD = 31.5, n = 44$; high protein: $\bar{x} = 56.7, SD = 9.76, n = 83$). Mother's diet treatment was a significant coefficient when egg sac was treated as a random effect in survival analysis ($z = 2.41, P = 0.016$), with greater variation in the number of days it took the intermediate protein mother's spiderlings to reach both the 1st and 3rd molt (Table 12). However, since only six females produced spiderlings, it is difficult to determine the amount of influence from mother's dietary treatment versus the random effect of the egg sac on the development of offspring.

DISCUSSION

My data support the hypothesis that diet has large effects on life history, specifically reproductive outcomes and consequences for offspring, in the female triangulate cobweb spider. Of the 94 females in the study, 22 produced egg sacs, with 11 of these producing multiple egg sacs. However, only females fed a protein-enriched diet made viable egg sacs that ultimately produced surviving spiderlings. In addition, the analysis of a variety of dependent variables paints a consistent picture, with protein-enriched diets resulting in the best reproductive output for females, and increased survival and developmental rates for spiderlings. In models of female reproductive outcomes, the best performing models all included the female's diet treatment. In sum, this study provides strong evidence of the link between maternal diet and egg sac production in the triangulate cobweb spider.

Before discussing diet treatment, I will briefly consider the control variables (age and morphological measurements) that were related to female reproduction. Some females went through their molts at a faster pace than the other females leading to them being older at the beginning of the study. Each model showed that older females were more likely to produce egg sacs. However, faster pace of molting may have led to smaller increases in size between molts, resulting in smaller adult females. The size of the female had a negative impact on egg sac production, with smaller females having higher success, suggesting a possible trade-off between optimal molting rate and size. The initial weight of each female was positively correlated with whether or not females produced viable egg sacs, and also had a higher impact than female size. However, weight was not an important independent variable in other models. In other words, heavier females were

more likely to produce a viable egg sac, but smaller females were more likely to produce an egg sac and produced a higher number of egg sacs (viable and non-viable), suggesting a trade-off between the initial weight of the female and her size.

As protein is needed for egg sac production (Wilder & Rypstra 2010; Barry & Wilder 2013), I hypothesized that the protein-enriched diets would enable females to produce more egg sacs compared to the lipid-enriched diets. My data support this hypothesis with results showing that females in the protein treatments were more likely to produce an egg sac (viable or not) and a higher average number of egg sacs per female, than in other treatments. Studies of the effects of diet on egg sac production have produced mixed results. For example, similar to my study, Barry & Wilder (2012) found that female praying mantids on high-protein diets produced over twice as many egg sacs as females on high-lipid diet. However, Salomon et al. (2011) found no significant effect of diet on brood size and egg mass produced by female *Stegodyphus lineatus*, a subsocial spider. In this study the mass consumed from prey items (crickets) and the resulting body mass of females did not differ among diet treatments, which could explain the lack of an effect on brood size and mass. Previous studies performed on *S. lineatus* found that heavy females produced more eggs than lighter females (Salomon et al. 2005).

I also found that at the completion of the study trials, the lipid and protein content of the female spiders varied across diet treatments. Female spiders in the lipid treatments had a higher post-trial lipid content than females in the protein treatments. However, those females in the protein treatments had a lower post-trial protein content than females in the lipid treatments (Figure 6b). Females that had a lower post-trial content produced more egg sacs on average than those females with a higher post-trial protein content.

These results suggest that the females used the protein from their food source to produce egg sacs and there is a cost associated with egg sac production that has a potential effect on protein content of the females. The lipid content of the females on the lipid diet was very high at the end of the trial, which implies that they did not use the lipids they got from their diet. Other studies have suggested that opportunistic feeders may store lipids to buffer against periods of food deprivation by maintaining sufficient stores of energy to fuel metabolic needs between prey captures (Jensen et al. 2010). This is a common result due to their opportunistic feeding strategy (Jensen et al. 2010). Jensen et al. (2010) observed similar results in the wolf spider *Pardosa prativaga*. Their results show that wolf spiders did not adjust their metabolism to help maintain a constant body composition when prey nutrient composition varied (Jensen et al. 2010). Instead, the wolf spiders stored the extra lipids. This lack of metabolic adjustments may be adaptive in spiders that are occasionally exposed to unpredictable food availability (Jensen et al. 2010; Riechert & Harp 1987; Wise 1993).

In addition to fluctuations in food availability, activity levels of different spider species can affect what macronutrients are required in their diet. The triangulate cobweb spider is not a very active species compared to wandering spiders due to its sit-and-wait strategy of capturing prey. Web-building species might have higher requirements for protein, which is used for web building and tissue development during periods of growth (Wilder 2011). Since lipid is a much more effective source of energy due to its high energy density, those spiders that have more active lifestyles (wandering spiders) would be expected to have higher energy requirements (Wilder 2011).

Plant nectar is high in energy and nectar feeding occurs among all ages of spiders and among several different families (Pollard et al. 1995; Jackson et al. 2001; Taylor & Bradley 2009). Taylor & Bradley (2009) studied whether plant nectar could repay the energetic costs of wandering in two foliage wandering spiders. Their results showed that plant nectar increases survival, molting, and foraging in both species of spiders and concluded that non-web-building spiders that feed on nectar may utilize its energy for foraging and allocate the nutrients they gain from prey to maintenance and growth (Taylor & Bradley 2009).

Not only did female diet have an impact on her own reproductive output, but I found preliminary evidence that spiderling life history traits were also affected. There were differences found across mothers when her effect was included in the models, and although samples were small, the data show that the spiderlings produced by the mothers in the protein treatments differed in both their survival and development. The high protein mother's spiderlings had a higher survival rate through the first and final molt and also developed at a faster pace (reached their third molt in fewer days) than the intermediate protein mother's spiderlings. Several studies have found that spiderlings who are themselves fed higher protein content have faster growth and higher survival (Mayntz & Toft 2001; Jensen et al. 2011b; Salomon et al. 2011). Here, I have shown that even when spiderling diet is held constant, their life history may be directly impacted by the diet their mothers ingested before and during egg production. In nature, prey items available in different habitats lead to adult female spiders differing in their nutritional histories, which in turn may influence offspring fitness (Wilder 2011).

Little is currently known about spider nutritional requirements, despite the important role spiders play in community dynamics (Wilder 2011). The nutritional ecology of spiders includes which nutrients are required in a spider's diet and how these requirements are met in nature with the prey items that are available in different habitats (Mayntz et al. 2005; Wilder & Eubanks 2010; Wilder 2011). Within an ecosystem, the nutritional requirements of spiders may influence the species of prey that are consumed and will, therefore, affect arthropod communities (Wilder & Eubanks 2010; Wilder 2011). Clearly, triangulate cobweb spiders are quite successful at reproducing indoors in human households. In such environments, they consume a wider variety of prey taxa and are also utilize a range of habitat types in which to find a mate and lay egg sacs. To further investigate the role of protein in spider reproduction, future studies could expand the range of protein supplemented or examine particular micronutrients to study their effect on life history. I have demonstrated the potential for this species to be used in further studies of maternal effects. By studying life history strategies, I hope to help in understanding the finer details of nutritional ecology, for example, how maternal nutrition affects egg production and life history of offspring.

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TABLES AND FIGURES

Table 1: Literature review of diet manipulations in spiders.

Paper	Nutrient treatment	Traits	Findings
Taylor & Pfannenstiel 2009	Nectar supplemented to prey (eggs of <i>Helicoverpa zea</i>)	Spiderling development (<i>Cheiracanthium inclusum</i>)	<ul style="list-style-type: none"> • Spiderlings survived longer, molted more times, and almost all of the spiderlings became small adults when nectar was supplemented • Females reared on prey with added nectar also had higher fecundity
Jensen et al. 2011a	<i>D. melanogaster</i> varying in lipid:protein composition	Regulations of nutrients in juvenile <i>Pardosa prativaga</i> wolf spiders	<ul style="list-style-type: none"> • Spiders fed prey with high proportions of protein increased consumption compared to spiders fed on other prey types • When prey was protein rich, ingested protein was incorporated less efficiently into body tissue
Jensen et al. 2011b	<i>Drosophila melanogaster</i> raised on range of protein and lipid supplements	Instar duration and growth in two species of juvenile wolf spiders	<ul style="list-style-type: none"> • Those spiders fed prey with higher protein content had both a higher growth rate and a larger carapace
Mayntz & Toft 2001	<i>D. melanogaster</i> raised on 6 different diets: <ul style="list-style-type: none"> • Control • Dogfood • Vitamin mixture • Amino acid • Methionine • Fat 	Wolf spider (<i>Pardosa amentata</i>) spiderlings	<ul style="list-style-type: none"> • Growth rates increased on diet including 19 different amino acids or fatty acids+cholesterol or commercial dogfood. • Survival increased when reared on fruit flies from cultures containing 19 amino acids or methionine or dogfood. • Adding dogfood increased spider growth and survival more significantly than the addition of any other single nutrient. • Adult female flies from the dogfood culture were significantly heavier than females from the basic culture

Bilde & Toft 2001	Combinations of: three different aphid species and <i>D. melanogaster</i> reared on a supplement of crushed dog food	Adult linyphiid spider reproductive success	<ul style="list-style-type: none"> • Spiders fed the fruit fly diet produced significantly more eggs than those in the aphid-only diet groups. • Compared to the fruit fly diet groups there was a fast decline in egg sac and egg production in the single-species and mixed-aphid diet groups
Salomon et al. 2011	Range of protein and lipid supplements	Mother growth and development, and fecundity; Spiderling survival (<i>Stegodyphus lineatus</i>)	<ul style="list-style-type: none"> • Female spiders that were raised on the protein-enriched diet had an increase in body size compared to the mothers in the other diets • Mothers on the protein-enriched diet had higher offspring survival than mothers on the intermediate diet

Table 2. Diet table including nutrient content of *Drosophila melanogaster* for each treatment.

Treatment	High protein	Intermediate protein	Standard	Intermediate Lipid	High Lipid
Growth medium	3:2 Casein: Basic	1:4 Casein: Basic	Basic	1:4 Sucrose: Basic	1:2 Sucrose: Basic
L:P ratio	0.03	0.14	0.20	0.26	0.38

Table 3. Alternative models for whether or not a female produced an egg sac during treatment. Models shown are those supported by the data (Δ AICc score less than 4).

Model	Intercept	Age	Tibia Length	Treatment	Initial weight	K	AICc	Δ	Model Weight
1	5.11	0.045	-3.81	-7.16		4	99.5	0.00	0.240
2	6.94		-3.07	-6.61		3	100.0	0.45	0.191
3	-1.11	0.053		-6.63	-276.2	4	100.5	1.01	0.145
4	3.88	0.053	-2.81	-7.47	-143.8	5	101.1	1.61	0.107
5	-0.28			-5.09		2	101.2	1.65	0.105
6	1.72			-5.90	-163.8	3	101.6	2.10	0.084
7	6.75		-2.83	-6.64	-29.7	4	102.1	2.60	0.065
8	-2.51	0.028		-5.04		3	102.2	2.66	0.064

Table 4. Predictors of whether or not a female produced an egg sac.

Variable	Sign	Relative importance	Top 15 models
		$\Delta \leq 6$	
Treatment ¹	-	0.95	8
Tibia length ¹	-	0.59	7
Age ¹	+	0.54	7
Initial Weight	-	0.38	7

¹ These variables were in the top model

Table 5. Predictors of timing of first egg sac production.

Variable	Sign	Relative importance $\Delta_{\leq 6}$	Top 8 models
Treatment ¹	-	0.93	8
Tibia length ¹	-	0.58	4
Age ¹	+	0.57	4
Initial Weight	-	0.44	4

¹ These variables were in the top model

Table 6. Total egg sacs produced per female spider.

Variable	Sign	Relative importance	Top 15 models
		$\Delta \leq 6$	
Treatment ¹	-	1.00	8
Age ¹	+	1.00	8
Tibia length ¹	-	0.72	7
Initial Weight	-	0.41	7

¹ These variables were in the top model

Table 7. Predictors of whether or not a female spider produced a viable egg sac.

Variable	Sign	Relative importance	Top 15 models
		$\Delta \leq 6$	
Treatment ¹	-	0.87	8
Age ¹	-	0.91	8
Initial weight ¹	+	0.72	7
Tibia length	-	0.26	7

¹ These variables were in the top model

Table 8. Predictors of number of spiderlings hatched per female spider.

Variable	Sign	Relative importance	Top 15 models
		$\Delta \leq 6$	
Treatment¹	-	1.00	8
Age¹	+	1.00	8
Tibia length¹	-	0.68	8
Initial weight	-	0.31	8

¹ These variables were in the top model

Table 9. Generalized linear mixed model output table displaying whether or not spiderlings lived through their 1st molt, and includes treatment and egg sac (random effect).

Fixed	Estimate	SE	z-value	p-value
(Intercept)	-1.32	0.56	-2.36	0.018
Treatment	-1.50	0.88	-1.71	0.088
Random	Variance	SD		
Egg sac	1.68	1.30		
Number of observations	192 (spiderlings)	15 (egg sacs)		

Table 10. Cox mixed-effects model output table displaying days to 1st molt, and includes treatment and egg sac (random effect).

Fixed	Coefficient	SE(coef)	z-value	p-value
Treatment	0.58	0.92	0.63	0.53
Random	Variance	SD		
Egg sac	3.02	1.74		
Number of observations	192 (spiderlings)	15 (egg sacs)		

Table 11. Generalized linear mixed model output table displaying whether or not spiderlings lived through their 3rd molt, and includes treatment and egg sac (random effect).

Fixed	Estimate	SE	z-value	p-value
(Intercept)	-0.20	0.49	-0.42	0.675
Treatment	2.14	0.76	2.82	0.004
Random	Variance	SD		
Egg sac	1.38	1.18		
Number of observations	192 (spiderlings)	15 (egg sacs)		

Table 12. Cox mixed-effects model output table displaying days to 3rd molt, and includes treatment and egg sac (random effect).

Fixed	Coefficient	SE(coef)	z-value	p-value
Treatment	1.87	0.78	2.41	0.016
Random	Variance	SD		
Egg sac	1.96	1.40		
Number of observations	192 (spiderlings)	15 (egg sacs)		

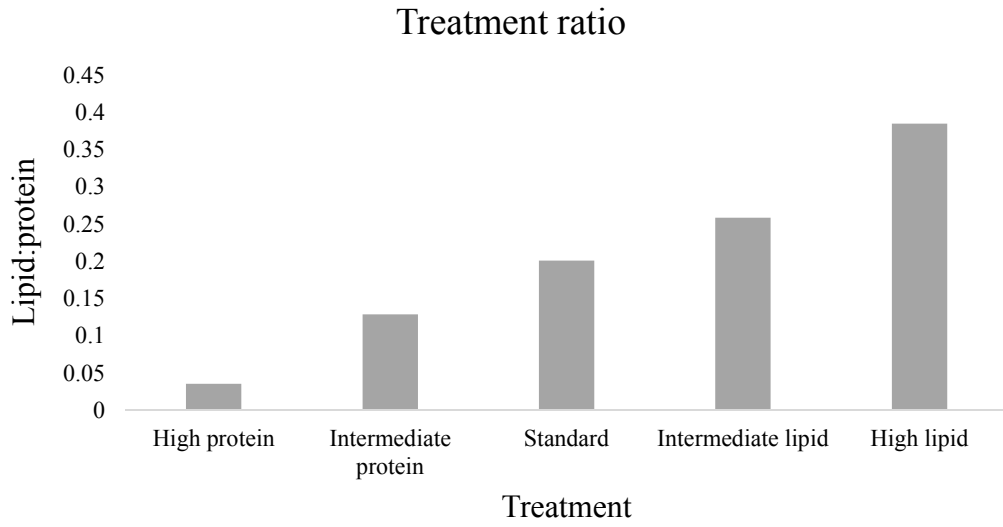


Figure 1. Lipid: protein ratio of flies from each treatment. The y axis displays the lipid: protein ratio and the x axis lists the five treatments.

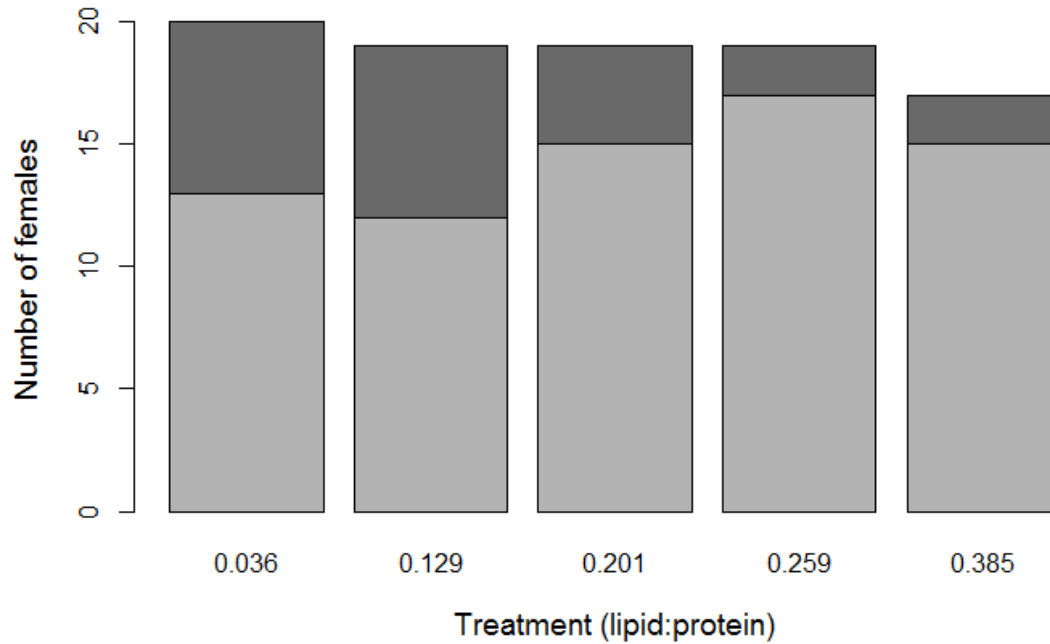


Figure 2. Whether female produced an egg sac by treatment. The treatment ratios are listed on the x axis and range from 0.036 (high protein) on left to 0.385 (high lipid) on the right. The dark grey shading represents the number of females that produced an egg sac in each treatment while the light grey shading represents the number of females that did not produce an egg sac.

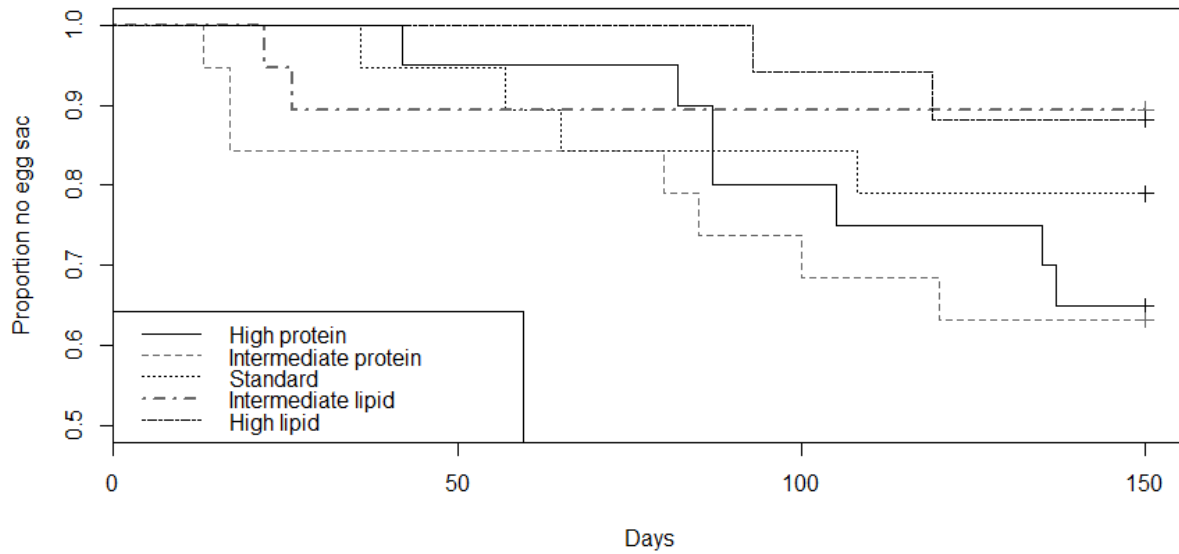


Figure 3. Kaplan-Meier survival curve for cumulative risk of not producing an egg sac by end of treatment. Crosses (+) at end of each treatment show right-censoring of females that had not produced their first egg sac by 150 days.

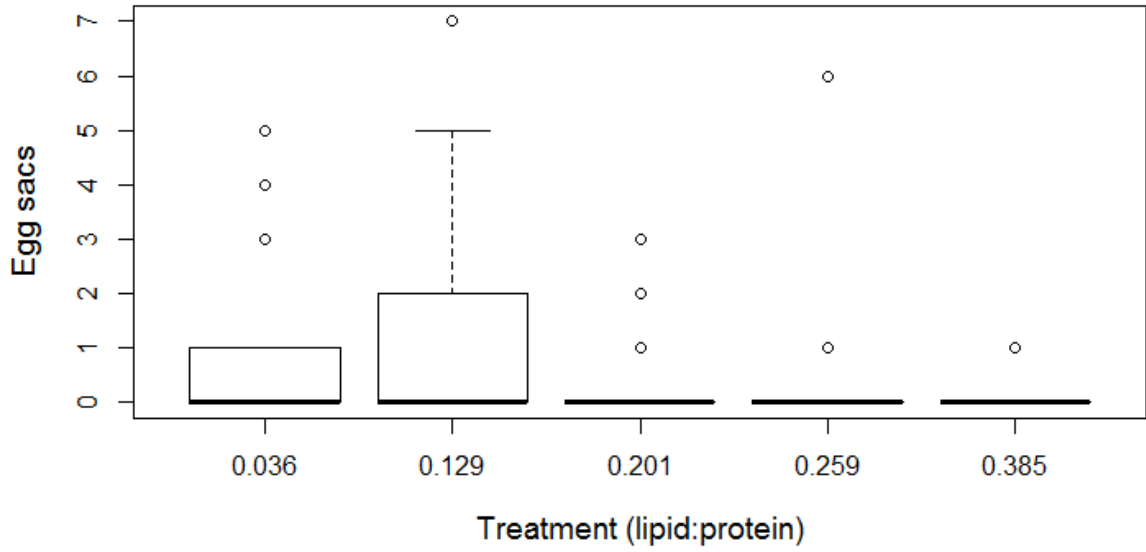


Figure 4. Total number of egg sacs produced per female. The treatment ratios are listed on the x axis and range from 0.036 (high protein) on the left to 0.385 (high lipid) on the right.

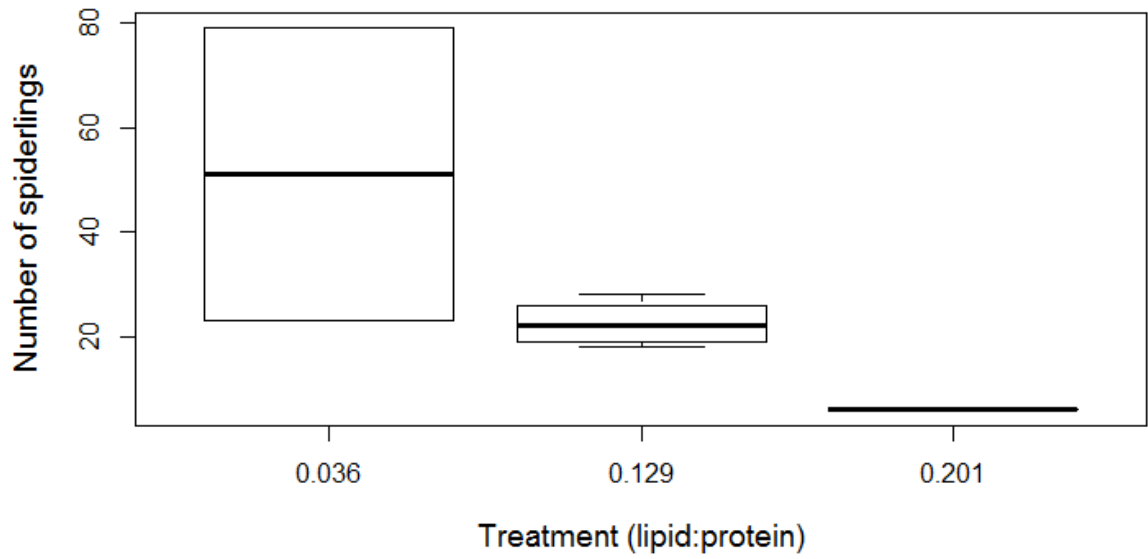


Figure 5. Total number of spiderlings hatched per female across treatments. The x axis displays the treatment ratios, ranging from 0.036 (high protein) to 0.201 (standard).

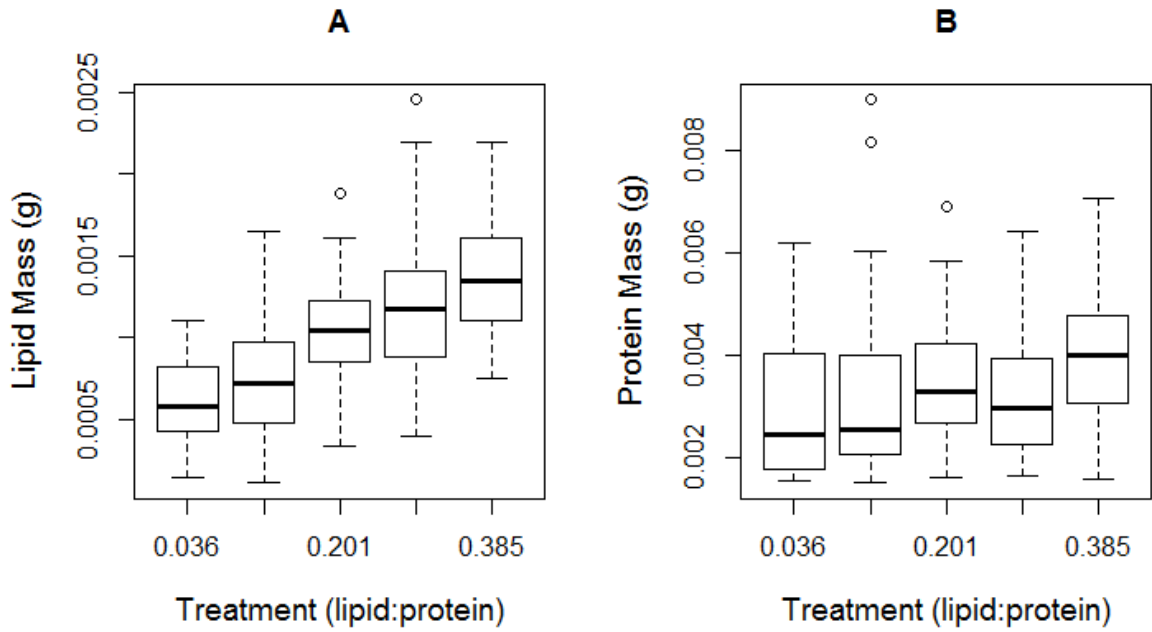


Figure 6. Lipid content (A) and protein content (B) of female spiders at the end of the study across treatments. Treatment ratios range from 0.036 (high protein) on left to 0.385 (high lipid) on the right.

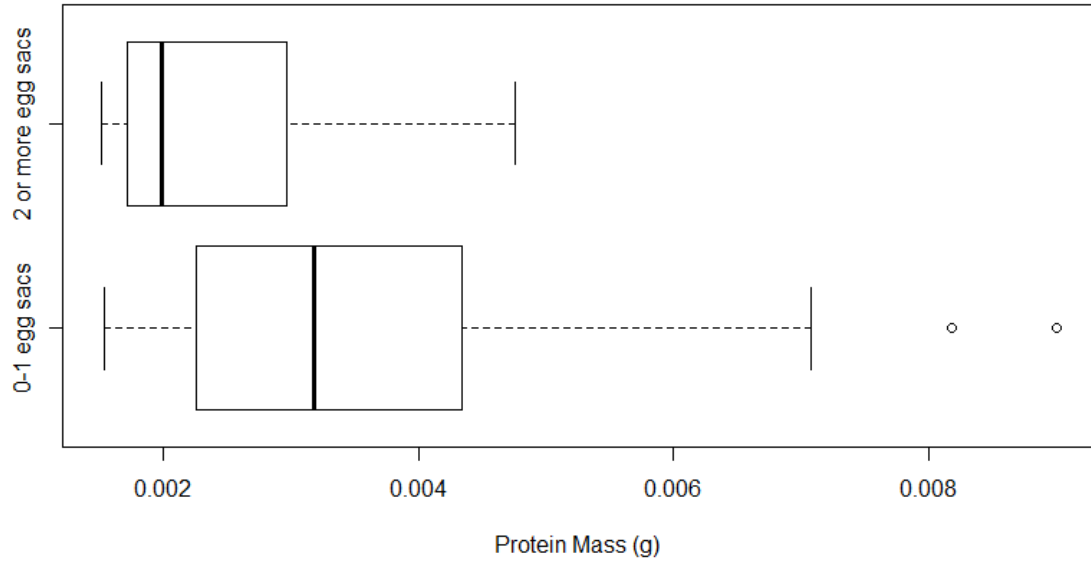


Figure 7. Relationship between egg sac production and the protein content of female spiders. The egg sacs produced are grouped into two groups: 0-1 and 2 or more.

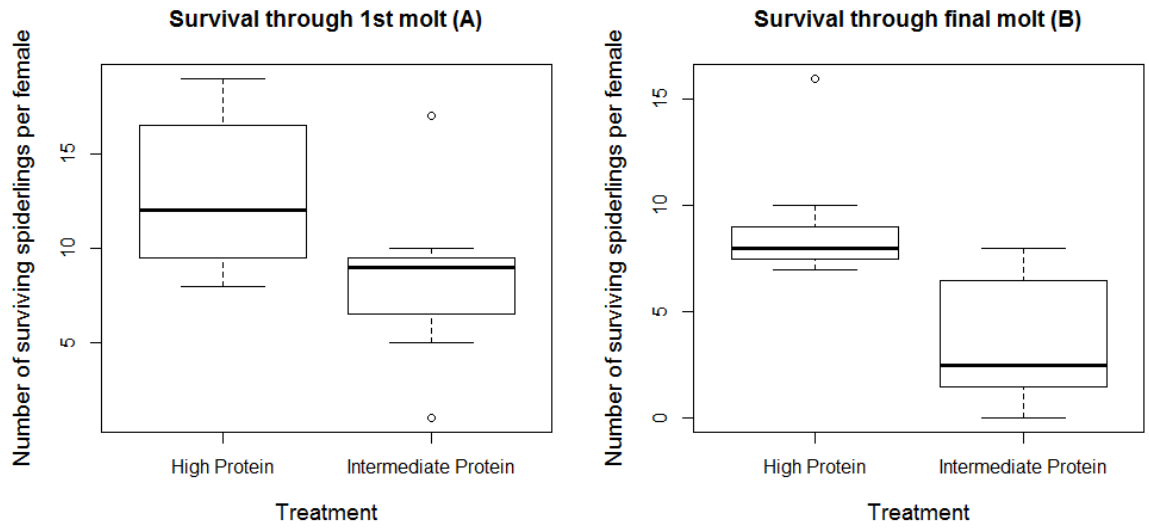


Figure 8. Number of surviving spiderlings per female through 1st molt (A) and 3rd molt (B) for intermediate and high protein treatments.

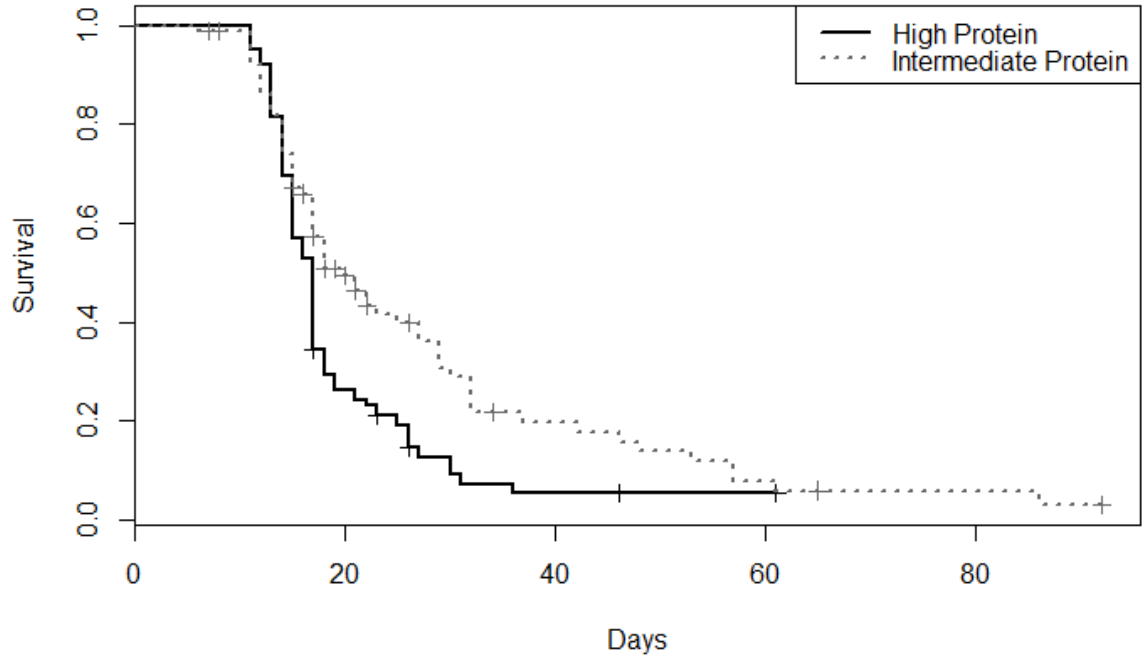


Figure 9. (A) Kaplan-Meier survival curve for total number of days from hatching to 1st molt. Crosses (+) indicate deaths.

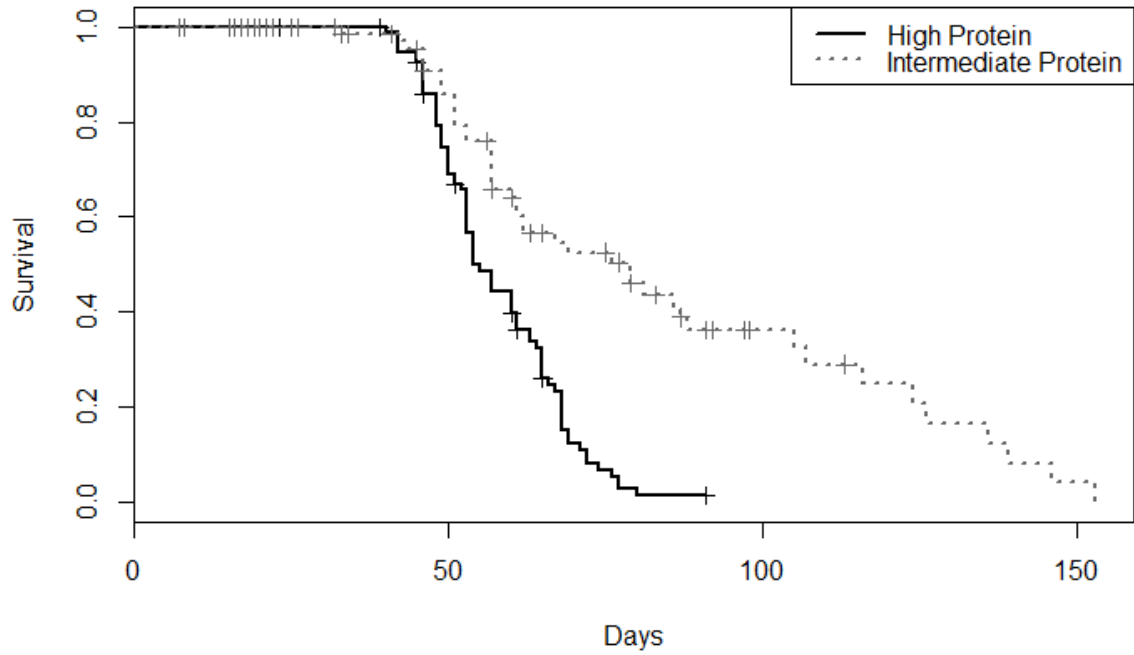


Figure 10. (A) Kaplan-Meier survival curve for total number of days from hatching to 3rd molt. Crosses (+) indicate deaths.

APPENDICES

Spider	Age	weight (g)	T. length	C. width	L.mass (mg)	P. mass (mg)	Trt	Yes/No Egg sac	Total Egg sacs	Yes/No Viable Egg sacs	Number of Viable Egg sacs	Number of spiderlings hatched	Number of male spiderlings	Number of female spiderlings
A008d10	146	0.011	2.3	1.26	0.011	0.257	4	0	0	0	0	0	0	0
A008d8	146	0.008	2.02	1.15	0.014	0.163	5	1	4	1	2	23	14	5
A012b2	123	0.007	2.2	1.13	0.020	0.352	4	1	1	0	0	0	0	0
A005g2	152	0.011	2.44	1.38	0.027	0.218	4	0	0	0	0	0	0	0
A009d8	137	0.011	2.03	1.12	0.028	0.178	5	1	3	0	0	0	0	0
A033e4	155	0.017	2.65	1.46	0.029	0.166	5	1	5	1	5	79	31	30

A005f3	134	0.016	2.6	1.35	0.034	0.353	3	0	0	0	0	0	0	0
A008b2	138	0.011	2.25	1.3	0.035	0.436	5	1	1	0	0	0	0	0
A006c8	130	0.012	2.13	1.3	0.040	0.157	5	0	0	0	0	0	0	0
A006c9	130	0.009	2.25	1.19	0.040	0.215	2	0	0	0	0	0	0	0
A006c6	130	0.009	2.1	1.16	0.043	0.606	4	0	0	0	0	0	0	0
A010b8	126	0.011	2.39	1.32	0.045	0.620	5	0	0	0	0	0	0	0
A012b3	123	0.01	2.27	1.18	0.046	0.154	4	0	0	0	0	0	0	0
A012b10	131	0.009	2.31	1.27	0.050	0.199	4	1	3	1	2	20	5	1
A009d7	131	0.010	2.1	1.16	0.050	0.420	4	1	5	1	2	24	5	3
A002f2	165	0.012	2.4	1.34	0.052	0.152	4	1	7	1	3	28	8	7
A007a10	140	0.011	2.06	1.18	0.052	0.183	4	1	3	0	0	0	0	0

A011a2	144	0.015	2.46	1.31	0.052	0.301	5	0	0	0	0	0	0	0
A029a4	150	0.013	2.35	1.26	0.054	0.177	5	1	1	0	0	0	0	0
A010b3	139	0.013	2.37	1.21	0.054	0.477	5	0	0	0	0	0	0	0
A003b1	138	0.013	2.35	1.28	0.055	0.352	2	0	0	0	0	0	0	0
A001b4	126	0.008	2.35	1.28	0.056	0.305	5	1	1	0	0	0	0	0
A009c3	145	0.014	2.3	1.29	0.060	0.189	5	1	1	0	0	0	0	0
A009a6	143	0.011	2.03	1.09	0.061	0.294	3	0	0	0	0	0	0	0
A003b7	138	0.015	2.58	1.35	0.061	0.411	2	0	0	0	0	0	0	0
A009a7	143	0.012	2.09	1.2	0.068	0.435	3	1	1	0	0	0	0	0
A011a6	138	0.012	2.38	1.31	0.072	0.209	5	0	0	0	0	0	0	0
A029a6	150	0.012	2.32	1.31	0.072	0.266	4	1	3	0	0	0	0	0

A003e3	144	0.012	2.28	1.29	0.074	0.243	3	0	0	0	0	0	0
A003c6	137	0.014	2.52	1.28	0.075	0.204	5	0	0	0	0	0	0
A008d4	139	0.008	1.93	1.08	0.075	0.478	1	0	0	0	0	0	0
A005f4	164	0.013	2.44	1.29	0.076	0.182	5	0	0	0	0	0	0
A003b4	145	0.014	2.33	1.29	0.079	0.161	5	0	0	0	0	0	0
A003a10	139	0.011	2.28	1.23	0.08	0.585	3	0	0	0	0	0	0
A002c8	146	0.010	2.04	1.16	0.083	0.334	2	0	0	0	0	0	0
A005f7	160	0.014	2.58	1.25	0.085	0.280	5	0	0	0	0	0	0
A010c4	123	0.010	2.23	1.26	0.086	0.251	4	0	0	0	0	0	0
A005f2	155	0.018	2.61	1.46	0.087	0.161	4	0	0	0	0	0	0
A003a5	147	0.011	2.26	1.23	0.087	0.227	2	0	0	0	0	0	0

A011b6	152	0.008	2.14	1.16	0.087	0.488	1	0	0	0	0	0	0	0
A012b6	137	0.008	2.03	1.08	0.088	0.345	1	0	0	0	0	0	0	0
A005f6	152	0.014	2.57	1.43	0.088	0.381	4	0	0	0	0	0	0	0
A012b5	131	0.011	2.2	1.22	0.089	0.312	3	0	0	0	0	0	0	0
A007a5	154	0.009	1.99	1.12	0.089	0.473	2	0	0	0	0	0	0	0
A010b1	139	0.013	2.46	1.31	0.090	0.318	5	0	0	0	0	0	0	0
A003c7	138	0.013	2.3	1.39	0.091	0.249	4	0	0	0	0	0	0	0
A004a9	145	0.011	2.3	1.29	0.092	0.257	2	0	0	0	0	0	0	0
A007a4	140	0.012	2.14	1.21	0.094	0.371	2	0	0	0	0	0	0	0
A010b4	132	0.011	2.15	1.24	0.094	0.499	3	0	0	0	0	0	0	0
A008a2	148	0.007	2.12	1.15	0.096	0.161	3	1	1	1	1	6	0	0

A007b7	134	0.015	2.44	1.34	0.096	0.436	5	0	0	0	0	0	0	0
A002c1	138	0.010	2.36	1.29	0.100	0.292	3	0	0	0	0	0	0	0
A006b8	140	0.011	2.24	1.26	0.101	0.425	1	0	0	0	0	0	0	0
A011b9	138	0.012	2.03	1.22	0.104	0.378	3	0	0	0	0	0	0	0
A006c3	138	0.011	2.4	1.25	0.104	0.459	4	0	0	0	0	0	0	0
A002c10	138	0.010	2.13	1.21	0.106	0.221	4	0	0	0	0	0	0	0
A004a10	137	0.011	2.44	1.3	0.106	0.450	5	0	0	0	0	0	0	0
A033e7	131	0.010	2.41	1.3	0.109	0.331	3	0	0	0	0	0	0	0
A006c10	124	0.010	2.1	1.16	0.110	0.158	1	0	0	0	0	0	0	0
A010b2	126	0.011	2.3	1.17	0.110	0.371	5	0	0	0	0	0	0	0
A010c9	147	0.011	2.27	1.21	0.111	0.176	3	0	0	0	0	0	0	0

A009c5	131	0.013	2.33	1.3	0.114	0.691	3	0	0	0	0	0	0	0
A010c2	131	0.009	2.12	1.18	0.116	0.430	2	0	0	0	0	0	0	0
A009c6	138	0.013	2.48	1.36	0.117	0.165	2	0	0	0	0	0	0	0
A007a8	140	0.009	2.11	1.22	0.117	0.209	3	0	0	0	0	0	0	0
A011c2	131	0.012	2.28	1.24	0.121	0.223	2	0	0	0	0	0	0	0
A003e5	150	0.012	2.32	1.29	0.121	0.348	1	1	1	0	0	0	0	0
A033e2	152	0.014	2.5	1.44	0.125	0.900	4	1	1	1	1	18	7	7
A009d3	131	0.010	2.26	1.23	0.127	0.255	4	0	0	0	0	0	0	0
A010c3	152	0.015	2.66	1.43	0.128	0.364	3	0	0	0	0	0	0	0
A010a8	139	0.013	2.29	1.2	0.128	0.433	1	0	0	0	0	0	0	0
A001a2	139	0.010	2.15	1.17	0.128	0.5449	1	0	0	0	0	0	0	0

A002a10	140	0.011	2.37	1.31	0.129	0.1750	2	0	0	0	0	0	0	0
A003e10	150	0.013	2.33	1.26	0.129	0.224	2	0	0	0	0	0	0	0
A002a5	140	0.011	2.16	1.3	0.133	0.608	2	0	0	0	0	0	0	0
A029a10	143	0.010	2.29	1.15	0.134	0.424	1	0	0	0	0	0	0	0
A011b3	139	0.011	2.31	1.24	0.137	0.263	1	0	0	0	0	0	0	0
A010b9	126	0.012	2.38	1.32	0.138	0.402	1	0	0	0	0	0	0	0
A011c10	139	0.011	2.31	1.2	0.148	0.275	2	0	0	0	0	0	0	0
A006c7	130	0.010	2.15	1.17	0.149	0.208	3	0	0	0	0	0	0	0
A011c9	145	0.011	2.33	1.24	0.149	0.297	1	0	0	0	0	0	0	0
A001c6	133	0.010	2.24	1.22	0.151	0.476	3	1	2	0	0	0	0	0
A005a1	160	0.012	2.07	1.16	0.152	0.643	2	0	0	0	0	0	0	0

A011b8	146	0.013	2.14	1.26	0.161	0.230	1	0	0	0	0	0	0	0
A012b4	131	0.011	2.3	1.23	0.161	0.412	3	0	0	0	0	0	0	0
A029a5	130	0.010	2.14	1.15	0.165	0.818	4	0	0	0	0	0	0	0
A011c8	125	0.011	2.32	1.31	0.180	0.316	1	0	0	0	0	0	0	0
A008d9	139	0.013	2.28	1.21	0.185	0.521	1	0	0	0	0	0	0	0
A001c3	133	0.012	2.11	1.22	0.188	0.297	3	1	3	0	0	0	0	0
A005a6	146	0.011	2.17	1.24	0.199	0.707	1	0	0	0	0	0	0	0
A008d7	139	0.011	2.31	1.26	0.215	0.376	2	0	0	0	0	0	0	0
A008a6	140	0.009	2.09	1.16	0.219	0.247	2	1	1	0	0	0	0	0
A005b1	145	0.013	2.21	1.24	0.219	0.309	1	1	1	0	0	0	0	0
A033e9 (ate male)	137	0.013	2.41	1.35	0.245	0.297	2	1	6	0	0	0	0	0

Appendix 1. Data from all females used in this study. The age column is the age (in days) the female was at the beginning of the trial. The weight column is her initial weight at beginning of trial. T. length and c. width are the tibia lengths and carapace widths of each

female as a measure of size. Lipid and protein mass are the lipid and protein content of each female at the end of the study. The trt column is the treatment each female was assigned to, ranging from high lipid (1) to high protein (5). Yes/no egg sac is whether or not (1/0) each female produced an egg sac. Total egg sacs is the total number of egg sacs each female produced. Yes/no viable egg sac is whether or not a female produced a viable egg sac and number of viable egg sacs is the total number of viable egg sacs produced per female. The number of spiderlings hatched is the total number of spiderlings produced per female. Number of male and female spiderlings columns show the number of males and female spiderlings produced by each female.

VITA

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Candidate for the Degree of

Master of Science

Thesis: HOW FEMALE DIET IMPACTS LIFE HISTORY TRAITS IN THE TRIANGULATE COBWEB SPIDER: EFFECTS OF NUTRITION ON FEMALES AND THEIR OFFSPRING

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