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The effect of diet on fecundity and survival of *Tidarren haemorrhoidale* (Bertkau, 1880) (Araneae: Theridiidae)

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Abstract. The range of trophic niches in spiders varies from very wide, including prey of several insect orders, other arthropods, and even nectar and other plant products, to very narrow, restricted to specific prey types, such as ants. Previous studies showed that the effects of a mixed diet are beneficial to fecundity, survivorship, and growth rate for some species but not others. This study evaluated the impact of a varied diet and monotypic diets of beetles, ants, and termites for *Tidarren haemorrhoidale* (Bertkau, 1880) a cobweb spider. Adult females were collected in a *Eucalyptus* plantation, kept in captivity, and divided into four experimental groups; each submitted to one of these diets for 125 days. Beetles were valuable prey for proteins and lipids compared to the alternatives. Termites and ants had equivalent contents of proteins, but termites were richer in lipids. Two monotypic diets composed of the main prey types (beetles and ants) had similar effects on fecundity and body mass compared to the mixed diet. Although termites have more lipids than ants and have a higher proportion of their biomass consumed, the monotypic diet of termites caused weight loss for spiders over time and reduced fecundity. Survivorship in all groups was similar. These results indicate that a diversified diet is not required for *T. haemorrhoidale* to achieve its maximum reproductive potential. This characteristic may be important to ensure the success of this species in colonizing and establishing large populations, even in disturbed habitats with low prey diversity.

Keywords: Diet specialization, nutritional quality, egg production, weight gain

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Stenophagous or oligophagous predators may physiologically specialize in the consumption of one or few prey items that fulfill their nutrient requirements, while euryphagous predators may achieve their nutritional balance by mixing many types of prey (Pékar et al. 2010; Terraube et al. 2011; Toft 2013; Pompozzi et al. 2018). The assessment of diet quality should consider all aspects of the prey's nutritional composition (including energy content and essential nutrients), defined as the prey's contribution to the predator's fitness (Toft 1999; Toft & Wise 1999a, b). It also involves evaluating costs associated with capture and digestion, quantifying indigestible parts of prey, and identifying toxins, which can drastically affect the suitability of a specific item (Oelbermann & Scheu 2002; Wilder 2011). However, it is important to consider that different species (and sometimes individuals) may present distinct nutritional requirements and adaptations to exploit their prey efficiently (Hooker et al. 2017; Pekár et al. 2018; Araujo & Moura 2022).

Food quality is particularly important for terrestrial predatory arthropods because they are often limited by the low availability of some nutrients and may face prey shortages for extended periods (Wise 1993; Wilder & Rypstra 2008). In this group, food limitation and/or the lack of specific nutrients may interfere with several life history traits, such as growth rates, survivorship in different instars, and reproduction (Uetz et al. 1992; Toft & Wise 1999a, b; Oelbermann & Scheu 2002). Diet composition, however, may affect even closely related species very differently. Jensen et al. (2011a,b), for example, tested how the nutritional composition of prey affected the body condition and growth of juveniles of two cursorial spiders, *Pardosa amentata* (Clerck, 1757) (Lycosidae) and *P. prativaga* (L. Koch, 1870). They found that a protein-poor and lipid-rich diet increased the duration of the instars in *P. amentata*. *Pardosa prativaga* juveniles, on the other hand, can adjust capture rate and nutrient extraction in response to prey mass and nutrient composition of offered prey. They are adapted to acquire and maintain their diet's essential components, even during periods of prey shortage or when the availability of suitable items is restricted.

In addition, the nutritional status of spiders and the quality of captured prey may be critical in the reproductive process (Mayntz et al. 2003; Wilder & Rypstra 2008; Barry & Wilder 2013). The egg production in these animals is influenced by their body condition (Fritz & Morse 1985; Head 1995; Mayntz et al. 2003). Consuming high-quality prey items generally ensures an efficient weight gain in the pre-reproductive period, resulting in a higher fecundity for cursorial (Wilder & Rypstra 2008) and web-building spiders (Mayntz et al. 2003). Therefore, including several different prey types in the diet may represent access to a broader range of nutrients, optimizing the fulfillment of essential nutritional requirements, such as certain amino acids and lipids (Uetz et al. 1992).

Spiders of the family Theridiidae exhibit a wide range of diet breadths, from stenophagous species with diets restricted to or almost exclusively composed of ants (myrmecophagous species, e.g., *Euryopis formosa* Banks, 1908), termites (termitophagous species, e.g., *Chrosiothes tonala* (Levi, 1954)) or flies (dipterophagous species, e.g., *Cryptachaea* Archer, 1946 and *Phoroncidia* Westwood, 1835) (Eberhard 1991; Clark & Blom 1992; Pekár et al. 2012) to euryphagous species, which usually capture a wide range of prey types (Nyffeler et al. 1988; Knoflach & Harten 2006). *Tidarren haemorrhoidale* (Bertkau, 1880) females were previously reported capturing and consuming prey of eight insect orders in two localities of southeastern Brazil (Pitilin et al. 2020; Moura et al. 2023). In both cases, there was a great predominance of ants in the diet. In North American agroecosystems, this species was also observed feeding mainly on ants and aphids (Nyffeler et al. 1988; Moreno-Mendoza et al. 2012). The impacts of diet diversification on its life history traits have not been previously investigated.

In this study, we compared the effects of one mixed and three different monotypic diets on the weight gain, fecundity, and survival of *T. haemorrhoidale* collected from a population established in a *Eucalyptus* plantation. Considering that ants represent about 70% of the prey items captured by *T. haemorrhoidale* females in the population studied (Pitilin et al. 2020) and the results suggesting individual specialization in beetles or ants reported by Moura et al. (2023) in another population, we expected that monotypic diets composed of these two prey types would have similar effects on the spiders, compared to the effects of a mixed diet. Termites, conversely, are relatively rare prey, and we expect a reduction in weight, fecundity, and survival of individuals feeding exclusively on these insects.

METHODS

Study site.—Spiders were collected in a *Eucalyptus* plantation in Fazenda Nova Monte Carmelo (18°45′11″S, 47°51′28″W), Estrela do Sul, Minas Gerais, Brazil. Spiders were maintained in plastic containers (diameter × height = 18 × 18 cm) with *Eucalyptus* branches attached to the walls for web placement and wet cotton.

Study species.—*Tidarren haemorrhoidale* is distributed from the USA to Argentina (WSC 2022) and builds webs composed of a dense non-sticky tangle containing a refuge made of a curled dry leaf (Pitilin et al. 2020). The webs are usually attached to thin branches of trees and placed close to the trunks. Prey are usually intercepted by gum-footed threads attached to the substrate below the tangle.

Differential diets.—The experiment was conducted between August and December 2017. We initially collected 70 adult females without egg sacs in the field. All spiders were weighed, excluding the 15 lightest and the 15 heaviest. The remaining 40 females were randomly divided into four experimental groups, with ten females in each treatment: (1) diet composed exclusively of adult beetles (*Ulomoides dermestoides* Fairmaire, 1893 (Tenebrionidae), (2) diet composed solely of termite workers (*Nasutitermes corniger* Motschulsky, 1855 (Termitidae), (3) diet composed solely of ant soldiers (*Camponotus blandus* Smith, 1858 (Formicidae), and (4) mixed diet including all the prey types used in the other groups. The last group received only one type of prey in each feeding event. We collected termites and ants at Universidade Federal de Uberlândia, MG, Brazil. Beetles were reared in the laboratory.

To standardize the food available for spiders in each group, we first evaluated how much tissue could effectively be extracted from each prey type. For this, we kept 12 spiders without food for three days. Four of these individuals then received one termite each, four received ants, and four received beetles. The insects were weighed before, and their remains after the feeding event. Based on the results obtained, we decided to feed the experimental groups with one beetle, one ant, or two termites. Thus, the total biomass available to be extracted by the spiders was similar between the experimental treatments. Individuals from all groups received prey every other day. The experiment was conducted for 125 days, from August 11 to December 14, 2017. All spiders were weighed weekly after the 40th day (September 19) to evaluate differences in weight gain among groups. All the egg sacs deposited by females were removed, and eggs were counted using a stereomicroscope Leica M205C.

Table 1.—Bromatological analysis of prey types (mean and standard deviation).

Prey type	% Moisture	% Proteins	% Lipids	Lipid:Protein ratio
Beetle	51.00 ± 0.06	21.43 ± 0.32	11.50 ± 0.16	0.54
Termite	73.25 ± 0.20	15.77 ± 0.23	4.87 ± 0.09	0.31
Ant	72.90 ± 0.09	15.18 ± 0.16	2.27 ± 0.17	0.15

Prey nutritional content.—To determine the nutritional composition of each type of prey, we conducted a bromatological analysis quantifying the moisture, protein, and lipid contents. Nine grams of each prey were sent to the bromatological laboratory LaborNutri to analyze the nutrient contents. Proteins were quantified using the Kjeldahl standard protocol (FAO 2003), and lipids were quantified using a Soxhlet extractor after Smith & Tschinkel (2009). Moisture was determined by the difference between the weight of samples before and after drying in an oven at 105°C for 8h.

Statistical analysis.—We tested the effect of diet on weight changes using a generalized linear mixed model with Gamma error distribution and log link function. We included spider weight as the response variable, diet treatment, experimental days and their interaction as predictor variables, and female identity as a random variable. We built the model with the "glmer" function of "lme4" package (Bates et al. 2015) and calculated *P*-values using "Anova" function of "car" package (Fox & Weisberg 2019). We compared differences between slopes using "lstrends" function of "emmeans" package (Lenth 2022). We used the trigamma method to calculate conditional and marginal pseudo-R^2, representing the variance explained by the entire model and the fixed effects, respectively (Nakagawa et al. 2017).

We conducted an ANOVA to test the effect of diet (predictor variable) on fecundity (response variable) using the "lm" function of R base packages. To evaluate the effect of diet on female survivorship, we performed a Kaplan-Meier survivorship analysis and compared female survivorship between groups using a log-rank test in "survival" (Therneau et al. 2000) and "coin" packages (Hothorn et al. 2006). All statistical analyses were conducted in R, version 4.1.3 (R Development Core Team 2022).

RESULTS

Beetles presented the highest relative amount of both proteins and lipids. Termites and ants had similar protein content, but termites had two times more lipids than ants (Table 1). In addition, beetles and termites had a greater percentage of their biomass consumed (around 85%) compared to ants (76.6%; Table 2).

At the beginning of the experiment, spiders in all groups presented, on average, similar weights ($F_{3,40} = 0.40$, $P = 0.748$), but the weight differed among groups at the end of the experimental period. There was an interaction between diet treatments and experimental days (Intercept: $\chi^2_1 = 7393.98$, $P < 0.001$; Days: $\chi^2_1 = 0.57$, $P = 0.451$; Diet treatments: $\chi^2_3 = 4.03$, $P = 0.258$; Interaction: $\chi^2_3 = 68.38$, $P < 0.001$). In the group that received only termites, female weight decreased over the duration of the experiment. In contrast, female weight remained unchanged, on average, in the others (Fig. 1). The entire model explained 53.5% of the variation in spider weight, of which 43.7% was explained only by the fixed predictors.

Table 2.—Mean weight (mg) and standard deviation of each prey before and after consumption by the spiders. The difference between these values was considered as the biomass consumed.

Prey type	Prey weight	Prey weight after consumption	Biomass consumed
Beetle	11.98 ± 0.43	1.83 ± 0.22	10.15 ± 0.34 (84.7%)
Termite	6.03 ± 0.79	0.74 ± 0.14	5.28 ± 0.81 (87.6%)
Ant	14.03 ± 0.61	3.28 ± 1.27	10.75 ± 1.02 (76.6%)

The number of eggs laid by females also depended on diet treatments ($F_{3,37} = 3.78$, $P = 0.018$). There was no difference between the "beetle diet" and "mixed diet" groups and between those groups and the "ant diet" group ($P > 0.05$; Fig. 2). However, the diet based on termites resulted in a reduced fecundity compared to the "beetle diet" and "mixed diet" groups. Still, it was not different from the "ant diet" group (Fig. 2).

During the experiment, 16 spiders died (six in the "ant diet" group, four in the "beetle diet" group, four in the "mixed diet" group, and two in the "termite diet" group). However, spider survival was not significantly different between groups ($\chi^2_3 = 2.23$, $P = 0.520$; Fig. 3).

DISCUSSION

Spiders exhibit a wide range of diet breadths (Pekár et al. 2011; Pékar & Haddad 2011; Pekár & Toft 2014). Some species are adapted to exploit the resources of a few prey taxa efficiently (e.g., Pekár et al. 2018), while others benefit from maintaining a diet composed of several distinct prey types, having access to complementary nutritional components (Bilde & Toft 2000; Sigsgaard et al. 2001; Mayntz et al. 2005). Our results indicate that a diversified diet is not essential to *T. haemorrhoidale*, but the adoption of a monotypic diet composed of a prey type that is rarely captured in natural conditions (termites) has a significant impact on weight gain and fecundity. Monotypic diets composed of beetles or ants had similar effects on these variables, and the results were also similar to those observed in the group that received a mixed diet.

Myrmecophagy is the most frequent type of stenophagy observed in spiders, occurring, for example, in species of Zodariidae, Gnaphosidae, and Theridiidae (Pekár 2004; Pekár & Haddad 2011; Líznarová et al. 2013). Spiders of the genus *Tidarren* Chamberlin & Ivie, 1934 have webs particularly efficient for catching insects that walk close to the trunk or soil where the silk threads are attached. The webs do not have threads with adhesive droplets throughout their length, as found in some other genera of the family (e.g., *Helvibis*

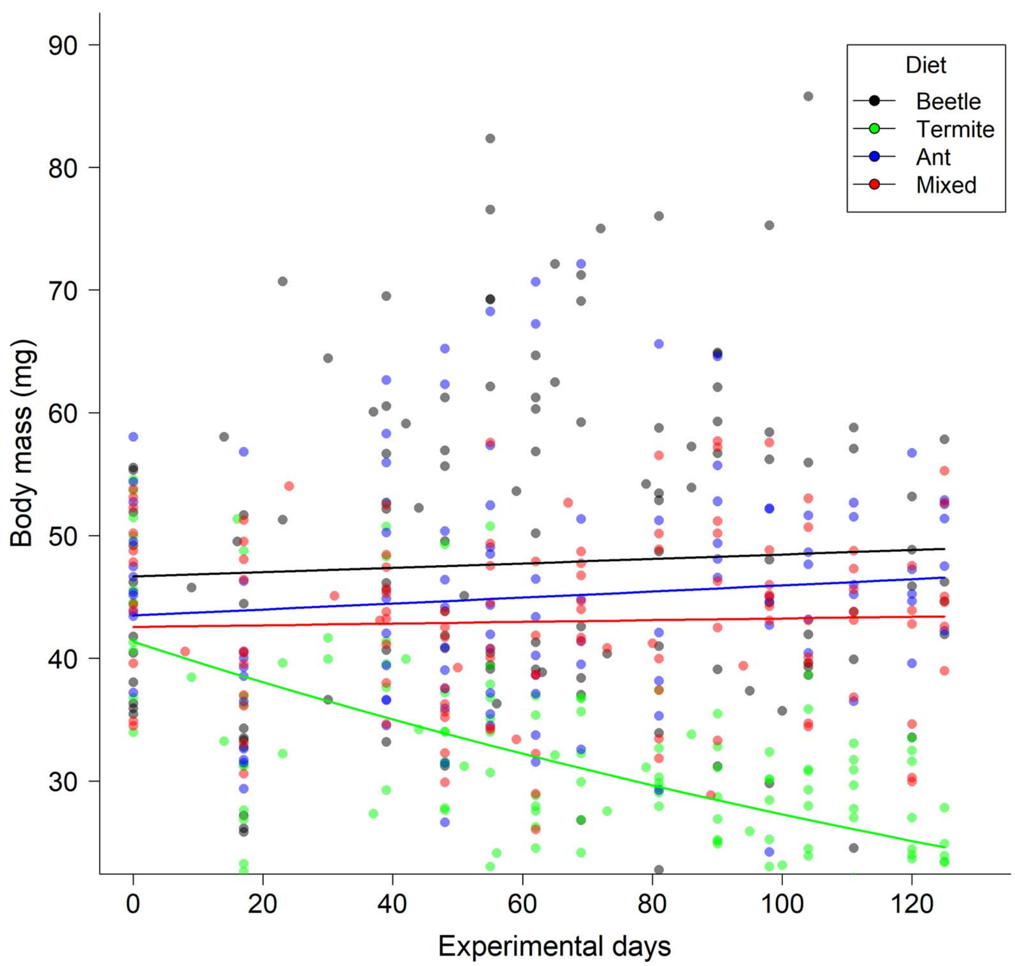

Figure 1.—Effects of diet treatments and experimental days on weight variation of *T. haemorrhoidale*. The female identity was included as a random variable in the model. The colors of lines and points represent the dietary treatment (beetle, termite, ant, and mixed diet).

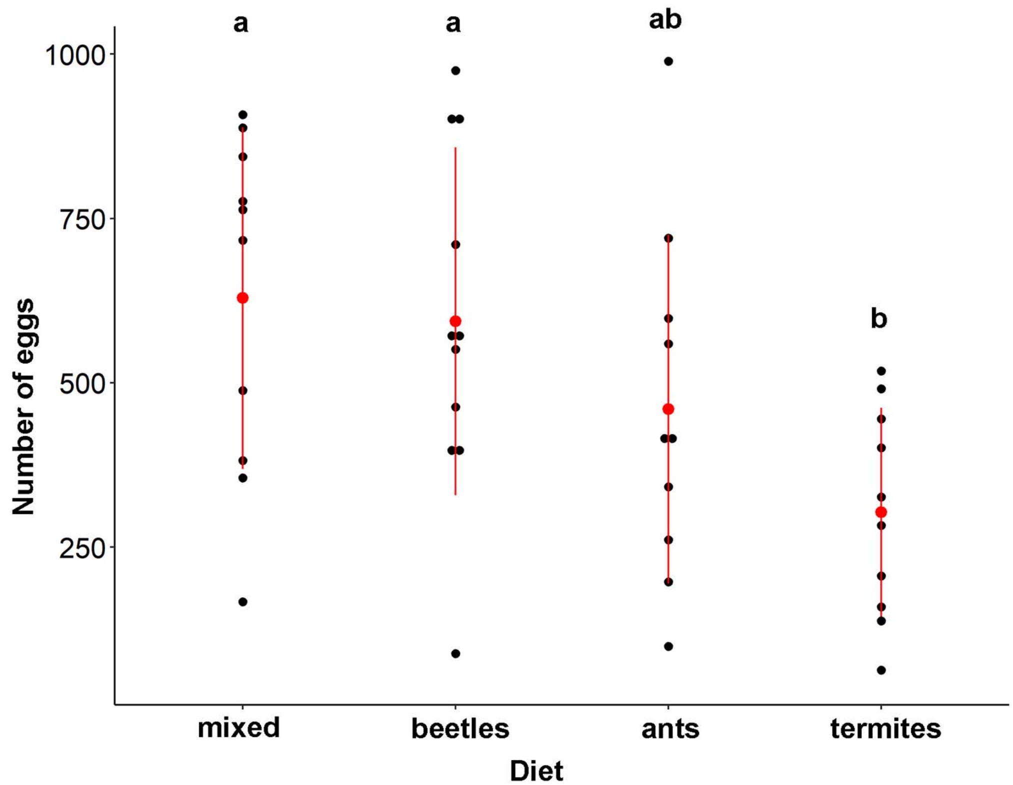

Figure 2.—Effect of diet treatments on egg production of *T. haemorrhoidale*. Red dots and lines represent means and standard deviation for each treatment, respectively. Black dots are the number of eggs produced by each experimental female. The same letters are not statistically different at $P < 0.05$ by Tukey's post hoc test.

Keyserling, 1884 and some *Chrysso* O. Pickard-Cambridge, 1882 (see Gonzaga et al. 2006). The webs of *Tidarren haemorrhoidale* may not be effective at capturing flying insects, but it is especially efficient in intercepting ants and, in lower proportion, other wandering insects (Pitilin et al. 2020). Still, it is physiologically able to survive and reproduce well with monotypic diets composed of other commonly available prey (beetles) or mixed diets. Ants were the main prey type of most females observed in a field study conducted in the Brazilian Atlantic Forest. Each individual, however, also captured a few other prey types. The results indicated that existence of a moderate individual diet specialization considering prey taxa and size (Moura et al. 2023). This empirical evidence supports our hypothesis that *T. haemorrhoidale* can be considered an oligophagous species. Foraging flexibility may allow individuals to eventually change their diets without compromising growth or fecundity, which may be an adaptative response to variation in the local availability of their preferred prey.

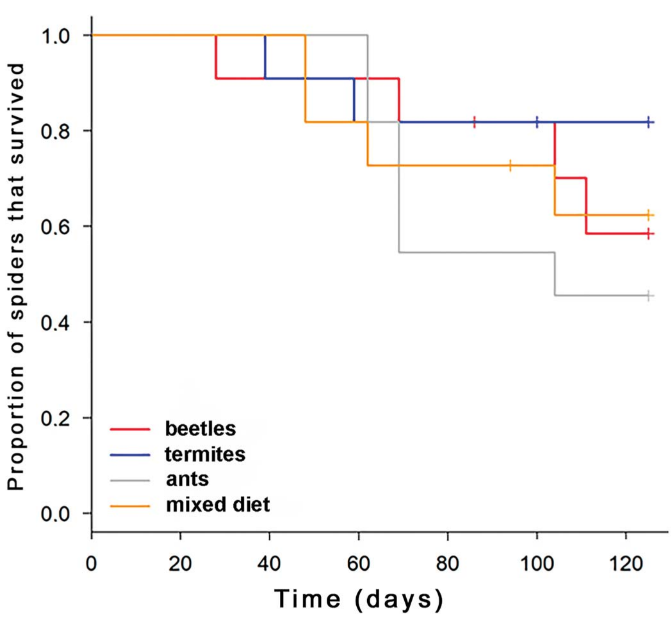

Figure 3.—Survival analysis of *T. haemorrhoidale* females submitted to four distinct diets in captivity for 125 days. The colors of lines and points represent the dietary treatment (beetle, termite, ant, and mixed diet).

Although the proportion of proteins was similar between the ants and termites used in our experiment, the latter had twice the proportion of lipids. The termite-based diet proved inefficient in promoting weight maintenance, resulting in lower egg production in *T. haemorrhoidale*. This result may be due to one or more of the following reasons: (1) termites may present a sub-optimal composition of nutrients (Mayntz & Toft 2001); (2) they may have harmful chemicals (Paradise & Stamp 1990); (3) the spiders may be inefficient in extracting or metabolizing nutrients from this prey type (Zschokke et al. 2006; Pekár & Toft 2009). Of course, the detrimental effects observed in the monotypic diet composed of termites in our experiment can be attributed only to *Nasutitermes corniger* workers, and divergent results are possible using other species and/or castes. Anyway, termites were not present in any web, although other species of spiders frequently caught these insects in the study area (Pitilin et al. 2020). Since they are not a common type of prey, it is possible that these insects may not be suitable to be included in the diet of *T. haemorrhoidale*. Other cases of the unsuitability of certain insects to feed other spider species have already been reported in the literature. For example, a diet based only on fly *D. melanogaster* negatively affects the development and fertility of lycosid spiders, apparently because these insects lack linoleic acids, which are essential nutrients for these spiders (Uetz et al. 1992). Therefore, spiders can present metabolic adaptations to increase extraction or efficiency in nutrient utilization when feeding on their preferred prey (Toft et al. 2010).

The impact of an unsuitable diet can also have important consequences on the mortality rate of predators (Mayntz & Toft 2001). When the spider *Portia fimbriata* (Doleschall, 1859) (Salticidae) was fed with the preferred prey (only spiders), most individuals survived to maturity (Li & Jackson 1997). However, when provided with other types of prey (mixed diets or just insects), the development time was longer, and the survival rate dropped dramatically. Our study did not find a relationship between diet quality and survival. Although the monotypic diet of termites decreased spiders' body mass throughout time and their fecundity, there was no increase in the mortality rate. Therefore, the spiders can obtain enough nutrients to survive, and adverse effects, if any, may only appear after a long time.

Our results confirm the existence of different responses on weight maintenance and fecundity according to the type of diet. The mixed diet can guarantee good results in weight maintenance and egg production; however, for an oligophagous species such as *T. haemorrhoidale*, monotypic diets can also satisfy its nutritional requirements, ensuring a good performance. Regarding future studies, investigating interindividual variation in diet within populations and possible differences in diets between populations will improve our knowledge of the physiological and ecological consequences of different diets for cobweb spiders.

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