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ORIGINAL ARTICLE

Effect of the nutritional quality of primary food on the development, sex ratio, and size of a parasitoid in a quadri-trophic food web

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Abstract. This study explores the effect of nutritional composition on the fitness of consumers in a quadri-trophic food web. Specifically, we studied how enrichment of the food of fruit flies *Drosophila melanogaster* (Meigen, 1830) transfers to the spider *Phylloneta impressa* (L. Koch) (Theridiidae) and its parasitoid wasp, *Zatypota percontatoria* Mueller (Ichneumonidae). We reared fruit flies on balanced, protein-enriched, and lipid-enriched diets, and observed several fitness-related traits in both the predator and the parasitoid. In spiders, we did not find significant differences among treatments in their body size and the probability of building a cocoon web. In parasitoids, we failed to find significant differences among treatments in the time to wasp pupation, the duration of pupation, the length of the wasp tibia and pronotum, and the body mass. However, the sex ratio of hatched wasps differed significantly among treatments from the expected 1 : 1. In the balanced diet group, the majority of wasps were males. There was a significant positive relationship between the spider prosoma size and the length of the wasp fore wing. Our results suggest that the quality of the food of the primary consumer had little effect on the fitness of the organism at the fourth trophic level.

INTRODUCTION

Food is the most essential resource, as it influences the growth, reproduction, survival, and metabolism of all animals (Wilder, 2011). Animals exposed to low-quality diets are more likely to show high-risk behaviours, e.g. predation (Moran et al., 2020), and compensate for the consumption of low quality food by increasing the amount of food consumed. Experiments with different qualities of diet have shown that consumers prefer high-quality food and, as a consequence, their growth and fecundity increases (Cruz-Rivera & Hay, 2000).

Changes in the nutrient composition of food for prey have a significant effect not only on primary consumers but also on predators (Mayntz & Toft, 2001). There is now substantial evidence available for tri-trophic food chains, in which a change in the diet composition consumed by prey influences, for example, the reproductive life span of the predator female. The quality of food consumed by prey correlates with a number of fitness parameters in predators, namely survivorship (Pedersen et al., 2002), growth (Kennish, 1996), and even silk decoration in orb web spiders (Blamires et al., 2009).

Most studies on nutritional ecology have focused on herbivores or predators, with very few on parasitoids. Because parasitoids exploit only one or a few hosts and gain nutrients only during ontogenetic (larval) development, their access to nutrients can be notably limited, particularly in parasitoids which have access only to nutrients provided by a single host. This is the case of ichneumonid parasitoids from the *Polysphincta* genus group, which are ectoparasitoids of spider hosts (Quicke, 2015; Broad et al., 2018). The parasitoid larva bites through the host cuticle and imbibes the haemolymph. During development, the larva obtains all nutrients only from the spider haemolymph, although, shortly before pupation, the larva finally consumes the whole body of the host, excluding the cuticle.

Host quality is determined by host age, size, sex, and nutritional status (Mackauer & Sequeíra, 1993). Larger hosts are more profitable than small hosts because they contain more resources to be utilised by the developing parasitoid larva (Harvey et al., 1994; Godfray, 1994). The quality of host resources affects the body size and survival of wasps, as well as the number of eggs available for oviposition in wasp females (Bai et al., 1992; Rivers & Denlinger, 1995). Specifically, adult wasp size is positively correlated with host size in idiobiont parasitoids (Harvey et al., 1998; Cloutier et al., 2000). The host size also influences the offspring sex ratio: it is shifted to more females in larger hosts and to more males in smaller hosts (Charnov et al., 1981; Favaro et al., 2018; Sequeira & Mackauer, 1992; Benamú et al., 2020).

The nutritional quality of a host can also affect parasitoid performance (Sarfraz et al., 2009). Ichneumonids are incapable of synthesizing their own lipids from carbohydrate sources; hence, they must obtain all fats from their host (Quicke, 2015). Lipids are stored in the haemolymph of their host (spiders in this case), which the wasp larva accumulates through wounds on the spider's abdominal cuticle. The protein and lipid content of the haemolymph of an individual arthropod can vary depending on its species, age, and nutrition (Cappelari et al., 2009). In a tri-trophic food chain, increased plant fertilization improves the quality of the herbivore host and consequently the parasitoid's fitness (Pekas & Wäckers, 2020).

Here we aimed to study nutrient transfer in a quadritrophic food chain. Specifically, we investigated whether different nutritional compositions of the food of the primary consumer would affect the fitness of the parasitoid. We hypothesised that if the host is able to regulate nutrient intake from its prey and consequently the wasp larva can selectively extract nutrients from its host, there should be little effect on the fitness of the parasitoid. We also investigated if the different diets can affect spinning activity of the spider host because quantity of silk produced depends on diet quality (e.g., Boutry & Blackledge, 2008).

METHODS AND MATERIAL

Insect and spiders

We used the ichneumonid wasp *Zatypota percontatoria* Mueller, which is an ectoparasitoid of juvenile theridiid spiders (Fitton et al., 1987; Korenko & Pekár, 2011; Korenko et al., 2016), to test our hypothesis. Development of the koinobiont larva of *Z. percontatoria* takes place externally on an active spider host, which is killed and consumed shortly before the larva's pupation (Korenko et al., 2016). The host species *Phylloneta impressa* (L. Koch) is an abundant generalist predator, which captures a variety of insects (Pekár, 2000).

Parasitised juvenile *P. impressa* spiders were collected by beating tree branches in an abandoned orchard in Brno (49.1558944°N, 16.5594158°E) in late September 2017. The parasitoid larvae were probably in the first instar. Individuals collected (N = 56) were placed singly in Eppendorf tubes with punctured lids and brought to the laboratory. Spiders were then placed singly in tubes (15 mm diameter, 60 mm long) with gypsum at the bottom, which was moistened regularly with a few drops of water, and the tubes were then plugged with a foam stopper. They were kept in a chamber under controlled conditions: 22°C, 12L : 12D.

Subsequently, the spiders were randomly assigned to three groups, each containing 18–19 individuals. Each group was fed with fruit flies (*Drosophila melanogaster* Meigen) reared on a different medium to achieve different nutritional compositions of flies (see below). Group 1 was fed with fruit flies on a balanced medium, group 2 was fed with fruit flies reared on a lipid-rich medium, and group 3 was fed on fruit flies reared on a protein-rich medium. The spiders were fed with a surplus of flies twice a week for a period of 85 days on average (47–171 days), until they were killed by the parasitoid. During this period each spider was offered in total about a hundred flies. The spider carcass was removed. The wasp larva and pupa were then reared under similar conditions (as above) until the imago emerged. The imago was then preserved by exposing it to ether.

We recorded the prosoma length of the spider carcass; whether the cocoon web, which provides protection to the wasp pupa (Korenko & Pekár, 2011), was constructed or not; the time to wasp pupation (from the start of the experiment); the duration of the pupal stage; the sex of the wasp imago; the mass of the wasp imago; the length of the wasp pronotum; and the length of the wasp fore wing and the fore tibia. Length measurements were conducted by means of an ocular ruler in an Olympus SX12 stereomicroscope. Mass was measured using a Kern 770 balance with a precision of 0.01 mg.

Experimental diets

Fruit flies were raised on three different media based on a mixture of a basic medium (Carolina Instant *Drosophila* Medium Formula 4–24) and casein (Sigma-Aldrich) or sucrose (Fluka). Lipid-rich flies were raised on a medium with a 1 : 4 ratio of sucrose and basic medium; balanced flies were raised on a 1 : 9 ratio of casein and basic medium; and protein-rich flies were raised on a 3 : 2 ratio of casein and basic medium. All flies were reared in 250 ml vials. A few drops of dissolved yeast were added to cover the surface of the medium. Cultures were inoculated with about 20 adult flies with mixed sexes and kept at 23°C. This procedure resulted in adult flies of variable protein and lipid compositions across the three dietary treatments (e.g., Mayntz & Toft, 2001).

Statistical analyses

The lengths of the spider prosoma, wasp pronotum, and wasp tibia, as well as the body mass of the wasp (following logarithmic transformation) were compared among treatments by means of a linear model (LM) of the ANOVA type, as the data showed a distribution not different from normal. Time to pupation was compared among treatments by means of generalised linear models (GLM) with a Gamma error structure; proportions of cocoon webs were compared among treatments by means of GLM with binomial errors (GLM-b); and pupal durations were compared using GLM with a Poisson error structure (Pekár & Brabec, 2016). A binomial test was used to compare the observed sex ratio frequency against the expected frequency. A Pearson correlation was used to study the relationship between spider prosoma size and length of wasp fore wing. All analyses were performed in the R environment, version 3.6.0 (R Core Team, 2019).

RESULTS

Effect on the host

The mean length of the spider prosoma at the time of killing by the wasp larva was not significantly different among treatments (LM, $F_{2,53}$ = 1.8, P = 0.18): it was, on average, 0.72 mm (SE = 0.009). The diet had no significant effect on the probability of building a spherical cocoon web (GLM-b, X^2_2 = 0.9, P = 0.63): on average, 64.1% (N = 53) of spiders built the cocoon web.

Effect on the parasitoid

All wasp larvae survived to final stage. The time to wasp pupation was not significantly different among treatments (GLM-g, $F_{2,53}$ = 1.9, P = 0.17): it was, on average, 84.5 days (SE = 4.68). There was also no significant difference in the duration of the wasp pupal period (GLM-p, X^2_2 = 0.2, P = 0.93): it was, on average, 8.8 days (SE = 0.1).

The sex ratio of emerged wasps differed significantly from the expected 1 : 1 only for the balanced diet group

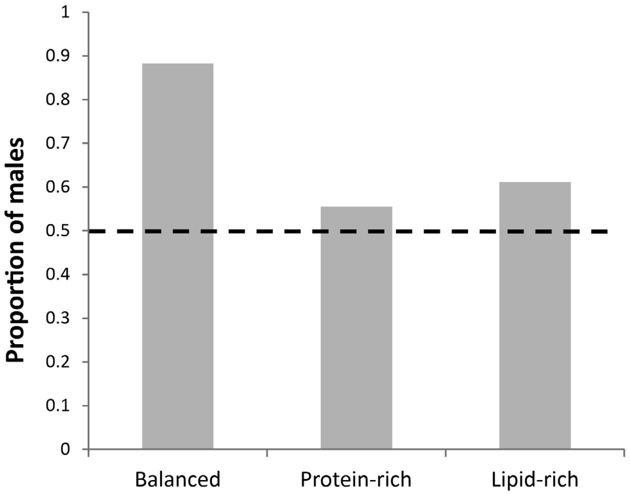

Fig. 1. Comparison of the proportions of hatched wasp male imagoes on three different diets. Dashed line marks the 1 : 1 sex ratio.

(group 1) (Binomial test, P = 0.002, Fig. 1), in which the majority of hatched wasps were males. In the other two diet groups (groups 2 and 3), the sex ratio was also in favour of males but not significantly different from 1 : 1 (Binomial tests, P = 0.41).

There was no significant difference in the length of wasp fore tibia (LM, $F_{2,49}$ = 0.4, P = 0.68): it was, on average, 0.97 mm (SE = 0.02). The length of fore tibia was not different between wasp sexes (LM, $F_{1,50}$ = 2.6, P = 0.11). Similarly, there was no significant difference in the length of the wasp pronotum (LM, $F_{2,49}$ = 0.9, P = 0.41): it was, on average, 0.44 mm (SE = 0.008). The length of the pronotum was not different between wasp sexes (LM, $F_{1,50}$ = 3.4, P = 0.07). Also, the body mass of wasps was similar among treatments (LM, $F_{2,49}$ = 0.1, P = 0.93): it was on average 0.67 mg (SE = 0.04). The length of fore wing of wasps was similar among treatments (LM, $F_{2,49}$ = 0.1, P = 0.90): it was on average 3.02 mm (SE = 0.05). The length of pronotum was significantly larger in males than if females (LM, $F_{1,50}$ = 5.3, P = 0.025, Fig. 2).

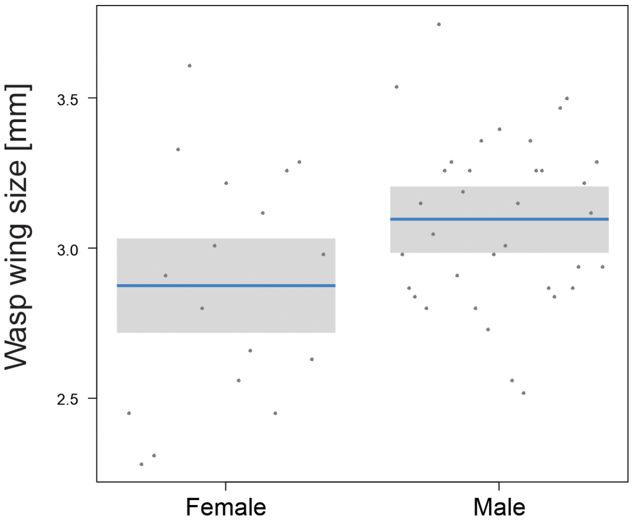

Fig. 2. Comparison of the wasp wing size between sexes. Blue line is the mean, boxes are 95% confidence intervals.

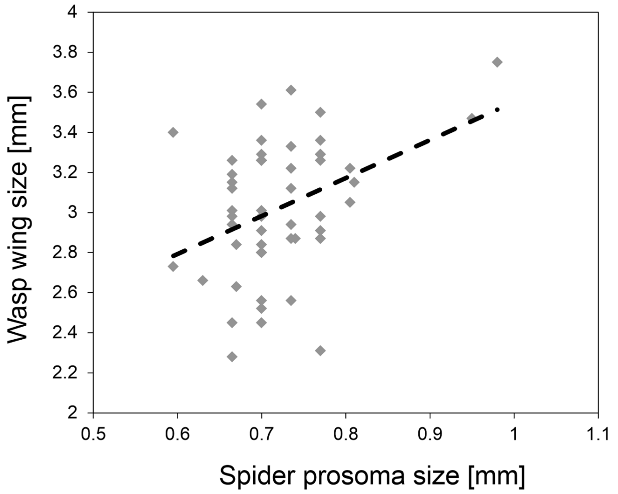

Fig. 3. Relationship between the spider prosoma size and wasp wing size. Black line is the estimated regression. Grey area is the 95% confidence band.

There was a significant positive relationship between the spider prosoma size and the length of the wasp fore wing (Pearson correlation, r = 0.34, t_{50} = 3.0, P = 0.004, Fig. 3) as well as the wasp pronotum (Pearson correlation, r = 0.31, t_{50} = 2.3, P = 0.027), and a marginally significant positive relationship between the spider prosoma size and the length of the wasp tibia (Pearson correlation, r = 0.28, t_{50} = 2.0, P = 0.046).

DISCUSSION

Parasitoids exhibit high efficiency with respect to food utilisation (Slansky & Scriber, 1985). In the present study, we investigated whether and how different nutritional compositions of the food of the primary consumer affect the fitness of the spider host and its parasitoid. We expected that the nutrient composition of the primary food would be reflected in the response of the parasitised host, as parasitoid development depends on the interactions with all lower trophic levels. We found that the majority of the studied life-history parameters of both the host and the parasitoid were not affected by nutrient imbalanced food, though the sex ratio was.

The regulation of nutrient uptake has been studied in a few host-parasitoid systems. Thomson & Redak (2005) found that parasitised host larvae failed to regulate macronutrient (protein and carbohydrates) intake when offered nutrient imbalanced food. This was in stark contrast to non-parasitised larvae, which altered their diet consumption in order to cope with nutrient imbalance (Thomson & Redak, 2008). However, both parasitised and non-parasitised larvae showed the post-ingestive regulation of protein utilisation. Parasitised larvae had less protein and, in particular, less lipid in their bodies compared to non-parasitised larvae (Thompson & Redak, 2008), suggesting that lipids were used to support parasitoid development. The reduction of fat reserves in parasitised hosts has also been reported for other systems (e.g., Dahlman & Green, 1981). This is related to the fact that wasp parasitoids are unable to synthesize their own lipids (Quicke, 2015). In our system, the growth of spider hosts was not affected by food enrichment. This could be because the parasitoid larva selectively extracted some host nutrients. Unfortunately, we failed to analyse the nutrient contents of both host remnants and adult parasitoids because the samples went astray.

Most spiders, as polyphagous true predators, must feed on a variety of prey to obtain the optimal nutrition necessary for successful survivorship (Uetz et al., 1992). For example, lycosids, by feeding on a mixture of prey species, obtained an optimal balance of nutrients (Greenstone, 1979). They select prey with optimal proportions of essential amino acids in their diet. There is plentiful evidence available showing the poor performance of predators when consuming prey fed on a nutrient-limited diet. For example, *Parasteatoda tepidariorum* (C.L. Koch) (Theridiidae) exhibited poor survival when fed with mealworms whose diet was limited to standard mealworm bran. When the mealworms were fed with vitamin-enriched commercial bran cereals, spider survival was higher, and spider growth faster (Walcott, 1963). This was probably due to the imbalanced content of two major macronutrients, lipids and proteins. It shows that the primary food content is reflected at the tertiary food chain level. The transfer of nutrients over several trophic levels has also been observed in other studies (Li & Jackson, 1997; Sigsgaard et al., 2001; Wen et al., 2020; Feng et al., 2022).

In our experiment, we used only one prey type (fruit flies), though studies suggest that spiders may need to consume different species of prey to attain a balance of nutrients (Greenstone, 1979; Mayntz et al., 2005). Yet, even a monotypic diet can provide optimal nutrients when enriched by additional nutrients. Evidence supporting this comes from a study on linyphiid spiders which were reared on nutritionally enriched fruit flies. Although the spiders were reared on the experimental diet for a period of two and half months on average, which is only about a third of their total developmental time, it covered most of the wasp developmental time. Therefore, we expect that the nutrients from the experimental diet could have been transferred from the host to the parasitoid. Spiders showed higher fitness when fed flies raised on enriched medium than spiders that were fed flies reared on normal medium (Bilde & Toft, 2000). Dog food added to the medium for fruit flies significantly increased spider growth and survival. Enrichment of food by lipids alone did, however, result in lower fitness when compared to enrichment by proteins (Feng et al., 2022).

Survival and development of the parasitoid are closely associated with the condition of their host, while the condition of the host strongly depends on the quantity of food available to it (Godfray, 1994; Thompson, 1999). Koinobiont endoparasitoids attack energetically suboptimal hosts, as the host grows to a larger size. It is known that parasitoids retard the growth of the host, resulting in a smaller body size compared to non-parasitised hosts (e.g., Thompson & Redak, 2008). If the host is starved, the parasitoid can perish. The body size of the adult parasitoid is positively related to host size (Salt, 1941). In addition, wasps from a starved host (*Drosophila melanogaster*) were smaller, though they developed faster (Wajnberg et al., 1990). Kishani Farahani et al. (2016) showed that the wing area of adult parasitoids was significantly affected by host age, this parameter decreasing with host age. In the present study, we revealed a significant positive relationship between the spider prosoma size and the length of the wasp wing. In our experiments, there were no significant differences in the size and body mass of the adult parasitoids among experimental diets, suggesting that the hosts on different diets were of similar energetic quality.

Silk products, as extended phenotypes of spiders, are composed of proteins; therefore, the amount of protein available to spiders should be reflected in the quantity and quality of their products. Blamires et al. (2009) showed that a high protein diet not only changed the fitness of the spiders but also changed their behaviour; specifically, it enhanced decoration building in an orb web building spider. Decorated webs increased the capture rate and consequently spiders with such webs grew faster (Li, 2005). In our study, we did not find significant differences in the probability of building a spherical cocoon web by the spiders. However, we did not study the cocoon webs in detail; thus, it is possible that the amounts of silk used to build the cocoon webs were different.

In parasitoids, the sex is determined at oviposition. If this was the case in our study then the biased sex ratio could be a result of female host selection at oviposition. Charnov et al. (1981) investigated the sex ratio as a function of the host size and found that females produced daughters on larger hosts and sons on smaller hosts. In our study, the hosts at the time of being killed by the parasitoid were of similar body size. We have, however, no data on host size at the time of oviposition. The sexes of the parasitoid could be biased by chance and the significant difference is a type I error due to a variety of reasons.

The sex ratio of wasps differed significantly from the expected 1 : 1 only for the balanced diet group (group 1). Therefore, it seems rather that the nutritional quality of the primary food must have affected the sex ratio by turning females into males. Indeed, in some species sex is determined by environmental conditions during ontogenetic development. Then biased sex ratios are expected and frequently observed (Charnov et al., 1981; Charnov, 1982; Werren, 1987). A number of factors have been identified to influence sex ratio in parasitoids (King, 1987). Among these, host quality should be important as other factors have been the same among treatments. For example, a female-biased sex ratio has been reported for parasitoids developing on a host feeding on food with higher nitrogen content (Fox et al., 1990).

Thus far, only a few studies have investigated the effect of diet in a quadri-trophic food-web. Quadri-trophic interactions were studied mostly in plant-herbivore-parasitoid-hyperparasitoid systems. Harvey et al. (2003) investigated the performance of parasitoids and hyperparasitoids when herbivores were fed plant species with different levels of secondary compounds. They demonstrated that the herbivore diet affected the survival not of the parasitoid but of the hyperparasitoid. Therefore, more studies on quadri-trophic interactions are needed to understand the effect of nutrients of the primary host for the fitness of parasitoids.

In conclusion, we found here that the quality of the food of the primary consumer had little effect on the fitness of the organism at the fourth trophic level.

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