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Benefit of actively mixing prey in a plant-inhabiting predatory mite

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Abstract. 1. Many animals can actively redress nutrient imbalances in their diet to maximise performance. However, food items are commonly patchily distributed in nature, thus, animals often need to commute between prey patches to mix their diet.

2. We previously found that females of two species of predatory mites showed a higher oviposition rate when feeding on a mixture of eggs of co-occurring phytophagous mites than on each prey separately. Besides, they searched for such a prey mixture on artificial arenas.

3. In nature, however, the two prey species are found on different parts of their host plant; hence, the predators need to commute between plant parts to obtain a mixed diet.

4. Here, we show that the reproduction of one of these predators was highest on mixtures consisting of various proportions of these prey, and was lower on single diets and on a mixture with a high proportion of one of the two prey. The predators consumed prey eggs in proportions differing from those offered, suggesting that they actively selected prey to obtain a mixed diet.

5. We found that the oviposition of the predator was lower on plants inoculated with either of the two prey species alone than on plants on which the eggs of the two prey species occurred on separate leaves of the same plant, forcing the predators to commute between the two prey.

6. We conclude that the predators actively searched for a mixed diet consisting of prey that were spatially separated on a plant.

Key words. Balanced diet, fitness, foraging behaviour, habitat structure, nutritional ecology, phytoseiids.

Introduction

Many arthropod predator species consume more than one prey species (Sabelis, 1992), whereas many herbivorous arthropods are specialised on a single host plant species or genus (Jaenike, 1990). Often, studies on diet choice of predators were based on the premise that predatory arthropods optimised the rate of prey capture or energy intake per time spent on a prey (Charnov, 1976a; Stephens & Krebs, 1986), but it has become clear that predators also use other criteria in choosing prey (Greenstone, 1979; Rapport, 1980; Tinbergen, 1981; Bilde &

Toft, 1994; Raubenheimer *et al.*, 2007; Jensen *et al.*, 2012). There are two explanations for the consumption of a mixed diet, and they are not mutually exclusive. One is that the animals need to mix their diet to dilute toxins present in one or more of the prey (Toft & Wise, 1999). Another explanation is that different prey species contain different amounts of nutrients and the predatory arthropods mix their diet to redress specific nutritional imbalances (Mayntz *et al.*, 2005). Both theories predict that animals should have higher fitness when they feed on a mixed diet than when feeding on each of the single diets.

Although there are many studies showing that arthropods actively redress nutrient imbalances in their diet, these studies often use semi-artificial diets or prey that were specifically reared to contain different amounts of nutrients (Mayntz

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et al., 2005; Raubenheimer et al., 2007; Dussutour & Simpson, 2009; Jensen et al., 2012; Vaudo et al., 2016; Raubenheimer & Simpson, 2018). Thus, evidence that arthropods do actively forage for a mixed diet consisting of several types of natural prey is scarce. Moreover, the different diets are often offered together, so animals do not need to cover distances to obtain a mixed diet (e.g. Raubenheimer et al., 2007; Jensen et al., 2012; Marques et al., 2015), and there are only a few examples of experiments where diet elements were spatially separated (Behmer et al., 2003; Mody et al., 2007; Ko et al., 2017). In nature, however, food items are commonly patchily distributed, and foraging costs (i.e. time and energy spent on commuting among prey patches) will increase with increasing distance between patches (Charnov, 1976b). Moreover, predators will have to spend more time and energy to obtain a mixed diet with increasing patchiness and habitat structure (Brown & Kotler, 2004). In summary, there is a lack of experimental studies on diet choice of arthropod predators that forage for natural prey that are patchily distributed. Here, we present a first example of this.

We previously found that the predatory mites *Euseius concordis* Chant and *Iphseiodes zuluagai* Denmark & Muma actively foraged for a diet composition consisting of two types of natural prey: the broad mite *Polyphagotarsonemus latus* (Banks) (Acari: Tarsonemidae) and the spider mite *Tetranychus bastosi* Tuttle, Baker & Sales (Acari: Tetranychidae). On artificial arenas where the two prey species were offered some distance apart, the predatory mites actively foraged for a mixture of the two prey species and had a higher oviposition rate on the resulting mixed diet than on each prey species separately (Marques et al., 2015). These herbivorous mites and predators co-occur, for example, on the biodiesel plant *Jatropha curcas* L. in Brazil (Sarmiento et al., 2011b; Pedro-Neto et al., 2013), where *P. latus* attacks the apical leaves and *T. bastosi* is mainly found on the old leaves (Rosado et al., 2014). Hence, predators need to commute between different plant parts to obtain a diet composed of the two prey species, from now on referred to as a mixed diet.

It is as yet unknown whether the two prey species are complementary in nutrient contents or whether toxins are present in the prey species. Thus, it is not possible yet to control the quality of the prey to construct a fitness landscape as a function of specific nutrients, as has been done for other species, using the geometric framework (Simpson & Raubenheimer, 1995; Simpson et al., 2004; Simpson et al., 2006; Behmer & Joern, 2008; Lee et al., 2008; Behmer, 2009; Jensen et al., 2012). We therefore first constructed a fitness landscape as a function of the proportion of the two prey species offered. As a fitness measure, we used the oviposition rate of predators, which is closely related to the growth rate of a population of offspring and life-time reproduction of predatory mites (Janssen & Sabelis, 1992). We investigated whether the predators consumed prey in different proportions from those offered, and whether oviposition rates were higher when the predators foraged for a composition of their diet that was more optimally mixed. Second, we investigated whether the predators performed better on plants on which the two prey species were offered together, but on separate leaves than on plants with only one prey species.

Materials and methods

The study system

The two phytophagous mites *T. bastosi* and *P. latus* are known to cause severe yield reductions and the predatory mite *E. concordis* is therefore being evaluated for its capacity to control these pests (Sarmiento et al., 2011b; Marques et al., 2018). *Tetranychus bastosi* is a typical tetranychid mite with adult females, the largest stage, being ca. 0.5 mm long (Sarmiento et al., 2011b). They feed on leaf cells by piercing them and sucking out the contents, thus forming chlorotic lesions. Their eggs are round, opaque, and ca. 0.13 mm in diameter. The broad mite, *P. latus*, is a very small tarsonemid (adult female 0.2 mm). They also pierce and suck out the contents of plant cells, causing virus-like damage symptoms. Only a few mites are sufficient to cause significant damage (de Coss-Romero & Peña, 1998). Their eggs are flat and oval and ca. 0.08 mm long. *Euseius concordis* is a phytoseiid mite that feeds on several prey species, such as tetranychid mites, broad mites, whiteflies, and eriophyid mites (de Moraes & Lima, 1983; Sarmiento et al., 2011a; Costa et al., 2014; de Alfaia et al., 2018). Adult females are ca. 0.3 mm long (Lofego, 1998).

Cultures

Jatropha curcas plants were grown in plastic pots (5 L) containing a mixture of soil and bovine manure (3:1) and were watered once per day. The herbivorous mites *T. bastosi* and *P. latus* and the predatory mite *E. concordis* were obtained from natural populations on *J. curcas* plants in Gurupi, State of Tocantins, Brazil (11°45'47"S, 49°02'57"W) in 2009. *Tetranychus bastosi* was cultured on *J. curcas* plants. The plants were kept in cages (47.5 × 47.5 × 93.0 cm) that contained a plastic tray (45 × 30 × 8 cm) that was placed inside a second tray (55 × 40 × 10 cm) filled with detergent and water, which served to prevent mite escapes and invasion of other arthropods. A clean plant was added to these cultures once a week and infested leaves of old plants were placed on it to allow the mites to move onto the new plant. The broad mite *P. latus* was cultured on isolated new *J. curcas* leaves (diameter ca. 5 cm), placed inside a plastic tray (45 × 30 × 8 cm) filled with distilled water with a sponge in the centre. A thin layer of wet cotton wool was placed around the leaves, which served to prevent mite escapes and desiccation of the leaves. Every 4 days, we replaced the leaves; the old leaves were placed on top of the new leaves. The predatory mite *E. concordis* was reared inside plastic boxes (11 × 11 cm) on flexible plastic disks (Ø = 6 cm) floating on distilled water. Small tent-like structures consisting of a folded piece of plastic with some cotton threads underneath were supplied on the arenas, serving as shelter, and oviposition site. Once per day, a small quantity of castor bean (*Ricinus communis*) pollen was supplied on the arenas as food for the predators (McMurtry & Scriven, 1964). All cultures were maintained in a climate room at 25 ± 2 °C, 65–70% RH and a LD 12:12 h photoperiod.

The optimal diet

The objective of this experiment was to assess the proportional mixture of prey eggs that maximised predator oviposition. We measured oviposition rates of individual adult female predators aged 9 days old since the egg stage (de Moraes & Lima, 1983). Using adult females of the same age is essential because the oviposition rate of predatory mites varies with age (Janssen & Sabelis, 1992). Experiments were carried out on leaves (diameter ca. 5 cm) inside plastic boxes (11 × 11 cm) filled with distilled water with a sponge fixed in the centre. A thin layer of wet cotton wool was placed around the leaves as above. We used eggs of the two prey species because mobile prey often display antipredator behaviour and this can affect the predation of the predator. To obtain these eggs, we transferred adult females of each prey species to a leaf with twice the number of adults that was required for each density. After 24 h, we removed all adult females of both prey species, leaving only eggs of each species at their respective densities. The surplus of eggs was removed with a pin to obtain the exact densities. We offered a mixture of eggs of both prey species in eight different combinations: 0/30, 5/25, 10/20, 15/15, 20/10, 25/5, 30/0, 60/0 (*T. bastosi*/P. *latus* eggs). Thus, the performance of the predatory mite was assessed with an increasing number of one prey species and a decreasing number of the other. To exclude the possibility that lower oviposition on a diet of only *T. bastosi* was caused by food limitation, we included the last treatment with twice the number of eggs of *T. bastosi* (60/0). The leaves with prey eggs were replaced daily with new ones with the same initial egg densities to maintain the prey ratios as constant as possible. Each density combination was replicated 16 times. The experiment was carried out in eight blocks in time, with two replicates of all treatments in each block. The number of prey eggs consumed during three consecutive days and oviposition of the predatory mite were assessed simultaneously. Because the oviposition of the first day is affected by the diet of previous days (Sabelis, 1990), we did not include oviposition and predation of the first day in the analysis.

The average numbers of eggs produced and the average predation by the adult female predators per day during the last 2 days of the experiment were analysed with a linear mixed-effects model (LME) with treatment as fixed factor and block as random factor (Pinheiro *et al.*, 2017). Treatments were compared through model simplification by aggregating treatment levels (Crawley, 2013). The proportions of prey eaten versus proportions of prey offered were analysed with a binomial test, and the oviposition of predators as function of the proportion of *T. bastosi* eaten was analysed with a linear and quadratic regression model. All statistical analyses were done with the statistical software R 3.3.3 (R Core Team, 2017). Models were checked by plotting residuals against fitted values and checking normality of the error distribution.

Mixed-prey diets on plant

The objective of this experiment was to assess whether the predatory mites indeed performed better on plants with both prey species than on plants with only one of the two species. Thirty-days-old *J. curcas* plants with four leaves were used. The

leaves of *J. curcas* are petiolate, alternate to sub-opposite with spiral phyllotaxis. Leaves were numbered from the youngest to the oldest leaf. The leaves attacked by *P. latus* and *T. bastosi* are the apical and middle third leaves, respectively (Rosado *et al.*, 2014). We previously found that 30 adult females of *P. latus* or *T. bastosi* produce enough eggs to feed one adult female of *E. concordis* during 4 days (Marques *et al.*, 2015). Therefore, 30 adult females of *P. latus* were transferred to the apical leaf (leaf one), and the third leaf from above received 30 adult females of *T. bastosi*. Control treatments consisted of *J. curcas* plants with the same prey species (*P. latus* or *T. bastosi*), again 30 females per leaf. When the plant was infested with broad mites, we released them on the two apical leaves (leaves one and two) and when the plant was infested with *T. bastosi*, the mites were released on the two lower leaves (leaves three and four). Thus, the predators had to cover slightly longer distances between leaves with prey on plants with both prey (i.e. between leaf one and three) than on plants with one prey (between leaf one and two or between leaf three and four). Moistened cotton wool was placed on the leaf petioles that received the prey to prevent them from moving to other leaves. After 24 h, we removed the moistened cotton wool and all adult females of the two species, leaving the eggs produced by the females behind. It was impossible to count the eggs of the two prey, especially those of *P. latus*, without damaging the plant. One adult female of *E. concordis* (9 days old since egg stage) was placed on the stem of the plant between the two leaves with prey eggs. The position of the predator was observed every hour from 1 to 5 h since release, and subsequently after 24, 48, 72, and 96 h. The oviposition of the predatory mite was recorded every day by carefully manipulating the plants under a stereomicroscope (Tecnival SQF-F, Brazil) and counting the eggs, which are much bigger than those of the two prey. We assessed the numbers of eggs of each prey species remaining on the leaves at the end of the experiment to ensure that sufficient numbers of eggs had been available throughout the experiment. Again, oviposition of the first day was excluded from further analysis. Each treatment was replicated 15 times. The experiment was carried out in five blocks in time, with three replicates of all treatments in each block.

The number of observed moves from one leaf to another was analysed with a generalised linear model (GLM) with a Poisson error distribution. The average number of eggs produced per day by the adult female predators on a plant was analysed with a linear mixed-effects model (LME) as above. The numbers of prey eggs of each species remaining per leaf at the end of the experiment were analysed with a GLM with a Gaussian error distribution. In the case of single diets, we used the average of the number of prey eggs remaining on the two leaves of the same plant. Treatments were compared through model simplification by combining treatment levels and comparing models using the 'anova' command in R (Crawley, 2013).

Results

The optimal prey composition

The total numbers of eggs consumed differed significantly among the ratios of prey species offered (LME, $\chi^2_7 = 24.0$,

$P = 0.0011$). The predator consumed lower numbers of eggs when offered 30 eggs of *T. bastosi* and none of *P. latus*, and higher numbers of eggs when offered 60 eggs of *T. bastosi* and none of *P. latus* (Fig. 1a). Equal numbers of eggs were consumed at all mixtures of prey species (Fig. 1a), suggesting that the predators substituted eggs of one prey with the eggs of the other prey, despite the eggs being of rather different sizes. At high densities of *T. bastosi*, predators consumed eggs in the same proportion as they were offered (Fig. 1a). However, with an increasing proportion of *P. latus* eggs offered, the predator consumed proportionally fewer *T. bastosi* eggs than offered (Fig. 1a).

The oviposition rate of *E. concordis* feeding on prey eggs varied significantly with the ratio of the two prey species offered (LME, $\chi^2_7 = 57.0$, d.f. = 7, $P < 0.001$). Oviposition was lowest when only eggs of *T. bastosi* were available, and highest when intermediate proportions of the two prey eggs were available (Fig. 1b), and a diet consisting of 83.3% (25/5) *T. bastosi* resulted in a significantly lower oviposition rate than the other mixed diets (Fig. 1b). The other mixed diets did not differ significantly from each other; hence, the optimal prey composition consisted of 16.7–66% *P. latus* (Fig. 1b). The oviposition rate of *E. concordis* varied significantly with the composition of the diet consumed (quadratic model, $F_{2,125} = 26.7$, $P < 0.001$) and the quadratic model fitted the data significantly better than a linear model ($F_{1,125} = 22.4$, $P < 0.001$), showing that there was indeed an optimal diet (Fig. 1b).

Mixed-prey diets on plants

The predators moved more between leaves on plants with both prey (average number of movements: 2.13 ± 0.26) than on plants with one prey (with *P. latus*: 1.87 ± 0.34 ; with *T. bastosi*: 1.47 ± 0.29), but this difference was not significant (GLM, $\chi^2_2 = 1.89$, $P = 0.39$). Oviposition of *E. concordis* differed significantly among treatments (Fig. 2, LME: $\chi^2_2 = 27.6$, $P < 0.001$). Oviposition was significantly higher with a mixed diet than with the single diets, and oviposition on a diet of *T. bastosi* was lower than on a diet of *P. latus* (Fig. 2).

The numbers of *P. latus* or *T. bastosi* eggs that remained per leaf at the end of the experiment did not differ among treatments (*P. latus*: single diet: 13.7 ± 1.75 eggs (average \pm SE), mixed diet: 15.6 ± 2.86 , GLM: $F_{1,43} = 0.35$, $P = 0.556$; *T. bastosi*: single diet: 37.0 ± 4.25 , mixed diet: 30.4 ± 6.56 , $F_{1,43} = 0.762$, $P = 0.387$). This shows that the numbers of eggs present were in excess of the numbers consumed and again suggests that they substitute eggs of one prey with the eggs of the other prey.

Discussion

Our results show that the predatory mite *E. concordis* benefits from mixing its diet on intact plants (Fig. 2a), but we did not observe significantly more frequent movement between leaves with prey on plants with both prey than on plants with one prey species. Whereas it has been amply shown that arthropods perform better on a mixed diet when the two diets are offered close to each other (Mayntz *et al.*, 2005; Raubenheimer

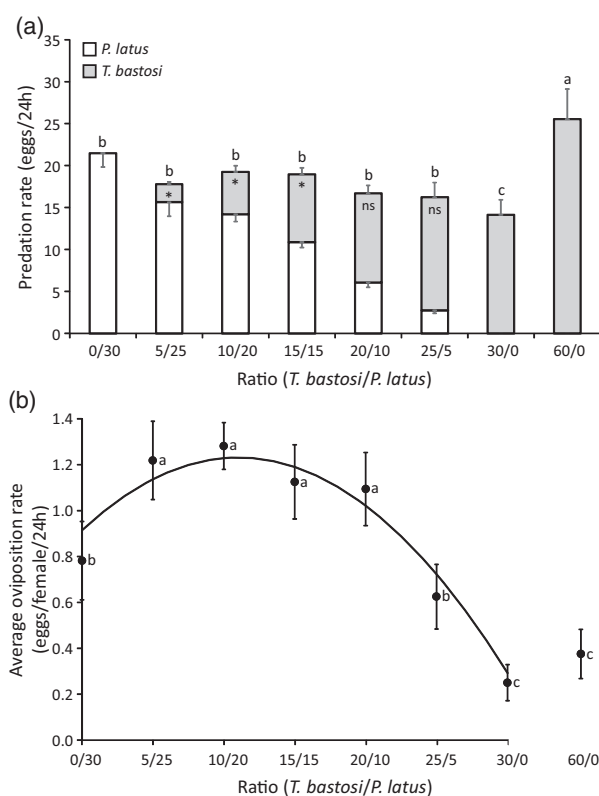


Fig. 1. (a) Predation rate (mean \pm SEM) of eggs of two prey species (*Tetranychus bastosi*, grey bars, and *Polyphagotarsonemus latus*, white bars) per day by *Euseius concordis* as function of the different proportion of prey eggs offered. Predation was assessed with an increasing number of *T. bastosi* and a decreasing number of *P. latus*. Letters above the bars indicate significant differences in total predation (i.e. predation of *P. latus* plus *T. bastosi*, contrasts after LME). Asterisks inside the bars indicate that the predators consumed a significantly lower proportion of *T. bastosi* eggs than offered, (binomial test, $*P < 0.05$, ns: not significant). (b) Average oviposition rate (\pm SEM) per day of *E. concordis* feeding on a diet consisting of different proportions of the prey species *T. bastosi* and *P. latus*. 0/60 indicates the treatment with twice the number of eggs of *T. bastosi* (i.e. 60 instead of 30 and no eggs of *P. latus*). Significant differences in oviposition rate are indicated by letters next to the averages (contrast after LME; $P < 0.05$). The curve is a fitted quadratic model of the oviposition rate as a function of the proportion of *T. bastosi* eggs consumed (Oviposition = $0.915 + 1.72x - 2.35x^2$, with x = the proportion of *T. bastosi* eggs consumed).

et al., 2007; Dussutour & Simpson, 2009; Jensen *et al.*, 2012; Raubenheimer & Simpson, 2018), there is not much knowledge on diet mixing in a more natural setting. Here, the predators had to search for the two prey on different plant parts, corresponding to the occurrence of these prey on small plants in the field. Although the predators presumably had to spend some time and energy to obtain a mixed diet, predators on a plant with eggs of both prey produced more eggs than predators on plants with only eggs of a single prey species and the average oviposition rate with a mixed diet on plants was comparable to that on leaves (cf. Figs 1b and 2a). The distance between the two prey species on the small plants used here is probably shorter than the distances

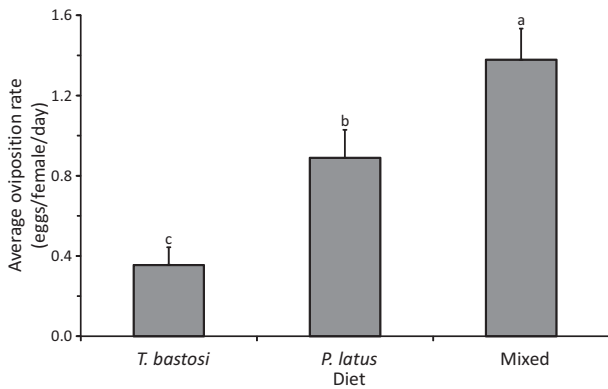


Fig. 2. Average oviposition (mean \pm SEM) per day of *Euseius concordis* on single- and mixed-prey diets on a plant. Plants contained *Tetranychus bastosi* plus *Polyphagotarsonemus latus*, each on a different leaf (mixed), or one of the two species on two leaves. Bars with different letters differ significantly (contrasts after linear mixed effects model, $P < 0.05$).

that the predator must travel to obtain mixed diets on large plants in the field. Clearly, more studies are required to show what happens on a large, full-grown plant in the field.

At high densities of *T. bastosi*, the predators consumed eggs in the same proportion as they were offered (Fig. 1a), but with an increasing proportion of *P. latus* eggs, the predators ate a lower proportion of *T. bastosi* eggs as was offered (Fig. 1a). We suggest that this was caused by predators selecting a mixed diet consisting of a higher proportion of *P. latus*, in agreement with earlier findings (Marques *et al.*, 2015). When *E. concordis* fed on a diet mainly or exclusively consisting of *T. bastosi*, it had a lower oviposition rate than on mixed diets and the oviposition rate of *E. concordis* was lower when the predators fed on single diets than on most of the mixed diets (Fig. 1b). The oviposition rate in the treatment with 60 eggs of *T. bastosi* was similar to that in the treatment with only 30 eggs of *T. bastosi*, showing that the lower oviposition rate when feeding on this prey was not caused by food limitation. Besides, the predators had the lowest performance when the plant contained only *T. bastosi* (Fig. 2b). It is unclear whether this is because *T. bastosi* is toxic to the predators or whether they are relatively deficient in some nutrients.

The oviposition rates of the predators did not differ among diets consisting of 16.7–66% of *T. bastosi* and the peak of the fitness curve (Fig. 1b) is relatively flat, suggesting that selection for obtaining the exact optimal diet is probably not strong. We suggest that there is selection for predators to mix some *T. bastosi* into a diet of *P. latus*. Elsewhere, we showed that *E. concordis* moved between patches more frequently when each patch harboured one of the two prey species than when both patches harboured the same species, hence, that predators actively searched for a mixed diet (Marques *et al.*, 2015). Here, we did not find such an effect. This was probably caused by the less frequent observations of the predator position in the current study (every hour during 5 h here and every 10 min in Marques *et al.*, 2015). Such more frequent observation of predator positions was impossible in the current study because

it would have caused too much disturbance due to frequent manipulation of the intact plants.

Our results also have practical implications. By foraging on a mixed diet on small plants, the predators increase their oviposition rate, resulting in the build-up of larger populations, which will result in better control of the two pest species on such small and vulnerable plants. The difference in oviposition is especially pronounced between a mixed diet and a single diet of *T. bastosi*. Hence, we expect that the predators will control this pest better in the presence of the other pest. There are now several examples of natural enemies that perform better on a mixed diet (Dean & Schuster, 1995; Evans *et al.*, 1999; Oelbermann & Scheu, 2002; Messelink *et al.*, 2008; Muñoz-Cárdenas *et al.*, 2014; Marques *et al.*, 2015), and such natural enemies may be more efficient at controlling pests when they can feed on such a mixed diet (Messelink *et al.*, 2008). In contrast, there are also studies showing that performance of predators on a mixed diet can be less good than on the single diets (Momen & Saway, 1993; Cañarte *et al.*, 2017), and it is still an open question why these predators feed on a mixed diet rather than on the best single diet. One of these studies concerns another species of predatory mite, but the same two prey species as used here (Cañarte *et al.*, 2017), showing that an optimal mixed diet for one species is a suboptimal diet for another species. We conclude that the performance of *E. concordis* is higher on a mixed diet of eggs of the prey *P. latus* and *T. bastosi*, and is also higher on plants where these prey occur spatially separated, even though this forces the predators to actively forage for a mixed diet.

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Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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