

Article

Plants for Fitness Enhancement of a Coffee Leaf Miner Parasitoid

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Abstract: The enhancement of pest control through the conservation of natural enemies in agricultural fields is called conservation biological control. One of the strategies used on this system is to introduce or manage plants that can provide food for natural enemies. We assessed the effect of feeding resources on the fitness of a coffee leaf miner parasitoid, *Proacrias coffeae* Ihering (Hymenoptera: Eulophidae), by evaluating the effect of different nectar resources on the survival of *P. coffeae*. To do so we used three flowering plants: *Bidens pilosa*, *Galinsoga parviflora*, and *Varronia curassavica*, and the leguminous shrub, *Senna cernua* Balb. H.S. Irwin & Barneby which produces extrafloral nectar. When feeding on the floral nectar of *V. curassavica* and on the extrafloral nectar of *S. cernua* the parasitoids increased their survival, however, no significant differences were found when feeding on *B. pilosa* and *G. parviflora*. We evaluated the effect of extrafloral nectar of *S. cernua* on the egg load of *P. coffeae* and found an increase in their egg load when exposed to the extrafloral nectar and with increasing age. Our results show the potential of *V. curassavica* and *S. cernua* as nutritional resources to enhance the fitness of the parasitoid *P. coffeae*, by increasing their survival. Based on the research study, it is evident that the introduction of feeding resources for *P. coffeae* in the coffee agroecosystem will increase their fitness as a potential biocontrol agent by enhancing their survival and reproductive potential.

Keywords: plant provided food; nectar; *Proacrias coffeae*; conservation biological control



Citation: Calderón-Arroyo, C.; Togni, P.H.B.; Pantoja, G.M.; Saenz, A.S.; Venzon, M. Plants for Fitness Enhancement of a Coffee Leaf Miner Parasitoid. *Agriculture* **2023**, *13*, 244. <https://doi.org/10.3390/agriculture13020244>

Academic Editor: Marco Valerio Rossi Stacconi

Received: 11 November 2022

Revised: 10 January 2023

Accepted: 16 January 2023

Published: 19 January 2023



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1. Introduction

Conservation biological control has been developed consistently in the tropics over the last decades [1–3]. Most of the advances have been possible due to successful experiences in understanding how natural enemy species or assemblages interact with local resources provided by companion and non-crop plants within or nearby the main crop [3]. This is directly related to the overarching goal of conservation biological control based on strategies for management practices that favor natural enemy attraction by increasing their fitness and impact on pest population control [4]. Such manipulation can be performed by the diversification of the vegetation to increase the provision of alternative and supplementary food sources, which increases the availability of resources and creates suitable conditions for the natural enemies to establish within the crop [5]. Nonetheless, the prospection of using companion plants as a vegetation diversification strategy continues to be a challenge, as it is important to select plants that are easy to handle while also benefiting natural enemy populations. Vegetation diversification must be accomplished with plant species that match the natural enemies' needs, including the accessibility to resources [3,6]. Feeding on floral resources may, directly and indirectly, affect parasitoid biology and efficiency. Adequate sources of nectar directly affect parasitoids' longevity [7], egg viability [8], foraging decisions [9], and time to start the flight [10]. Nectar feeding may also have an indirect effect

on parasitoid fecundity through an increase in their longevity, allowing them to find their host and oviposit for a longer period of time [11] and a direct effect by enhancing the parasitoid egg load (i.e., the total number of mature eggs in the ovaries) [12]. This could be particularly important for synovigenic parasitoids, in which adults emerge with a few mature eggs and continue maturing them over time [13]. In this sense, providing feeding resources for the parasitoids may increase their chances to oviposit and perform biological control in the field [13].

Several studies [14–18] found that increased plant diversity in coffee crops increased the parasitism rate of the coffee leaf miner *Leucoptera coffeella* Guérin-Ménéville (Lepidoptera: Lyonetiidae) [14–18]. The coffee leaf miner is one of the key coffee pests in Brazil. The most commonly used measure to manage this pest is chemical control [19]. Although several parasitoid species have been reported in coffee crops [20–24] their use in augmentative and conservation biological control strategies would be benefited by selecting plants that increase parasitoids' fitness, whether parasitoids were mass released or naturally attracted to the crop [25,26]. The natural parasitism of the coffee leaf miner may reach 34.17% in diversified agroecosystems [4]. This can be explained by the fact that in diversified agroecosystems there are more resources to attract, maintain, and reward natural enemy populations [27–30].

The coffee leaf miner parasitism increased with increased nectar availability in the extrafloral nectaries of *Inga subnuda* subsp. *luschnathiana* (Benth) T.D. Penn. (Fabaceae) in coffee agroforest systems [31]. The presence of *Varronia curassavica* Jacq. (Boraginaceae), *Inga edulis* Mart. (Fabaceae), and *Senna macranthera* (DC. ex Collad.) H.S. Irwin & Barneby (Fabaceae), and non-crop plants kept the coffee leaf miner populations under the economic threshold level, mainly due to the increase in the pest parasitism rate [17]. However, except for Rezende [31], those studies do not elucidate the functional role of any specific plant or the related mechanisms that could explain the benefits of plant diversity in coffee crops.

Coffee crops host an abundant number of non-crop plants, of which *Bidens pilosa* L. (Asteraceae) and *Galinsoga parviflora* Cav. (Asteraceae) are among the most common ones [17,32]. Both are annual Asteraceae herbs that provide floral resources throughout the year, presenting capitula with ray and disc florets that are narrow and long [33,34]. *Bidens pilosa* is known to provide nectar to pollinators and predators (e.g., hoverflies and ladybirds) due to its exposed and easily accessible flower morphology [27]. The leguminous plant, *Senna cernua* Balb. H.S Irwin & Barneby (Caesalpinioideae) possesses extrafloral nectaries, which are found in the base of the petiole and could be easily accessible for parasitoids [35]. The shrub *V. curassavica* known for its medicinal properties [36], has proven to selectively enhance the survival of the generalist predator *Ceraeochrysa cubana* Hagen (Neuroptera: Chrysopidae) without positively affecting the coffee leaf miner's survival [17]. Besides, it attracts several other natural enemy species [2]. Its floral morphology, with wide and open corollas, may present a highly accessible source of nectar for the parasitoids [37].

Among the parasitoids found in coffee crops, the species *Proacrias coffeae* Ihering (Hymenoptera: Eulophidae) is one of the most frequently found parasitizing the coffee leaf miner [21,38].

Here, we evaluated the potential of the plants *B. pilosa*, *G. parviflora*, *V. curassavica*, and *S. cernua* to provide food resources in order to increase the fitness of coffee leaf miner parasitoids, using *P. coffeae* as a model species. We selected these plants as they vary in accessibility to the nectar sources, which could differently affect *P. coffeae* fitness in terms of longevity and fecundity. We anticipate that feeding on plant nectar will increase parasitoid survival and egg load, and that extrafloral nectar and open wide corollas from *S. cernua* and *V. curassavica*, respectively, will be more beneficial to the parasitoid than Asteraceae plants due to nectar accessibility [7,39,40].

2. Materials and Methods

2.1. Coffee Leaf Miner Parasitoids Collection

Coffee leaf miner parasitoids were initially obtained from intact mined coffee leaves from Catuaí coffee variety with plants at complete maturity (nine years old). The leaves were collected in a small plot in the experimental field “Diogo Alves de Mello” of the Universidade Federal de Viçosa (20°48′45″ S; 42°56′15″ W), state of Minas Gerais, Brazil. The region is located in the Brazilian Atlantic Rainforest biome, which presents an average temperature ranging from 12 to 22 °C and annual rainfall ranging from 1300 to 1900 mm [41].

The leaves were collected once a week from June 2020 to August 2021 on different sections of the coffee plant. No pest control measures were applied to the plot during that time. In the laboratory, the leaves were placed individually in 350 mL plastic pots with their petioles inserted in vials with water to maintain their turgidity. The leaves were kept in the laboratory under ambient conditions (at 19 to 26 °C and 40 to 90% RH). The pots were checked daily until the emergence of the parasitoids. After emergence, the parasitoids were kept in 10 mL vials with ethanol 70%. *Proacrias coffeae* was the most common and easiest to rear of all the species collected. The genus *Proacrias* could be identified by a set of morphological traits, one of the most outstanding being “propodeum with modified median carina: either broadened and dorsally flattened or split posteriorly” [42].

2.2. Rearing of *Proacrias Coffeae*

Immediately after emergence, the parasitoids were identified and sexed (females have a more globular gaster than the males, and the males have a translucent region in the first segment of the gaster in ventral view). Couples were kept inside a 350 mL plastic pot with a drop of honey for 24 h. Following that, females were individually placed in 350 mL plastic glasses with a drop of honey in the glass wall and three mined coffee leaves. The leaves had their petioles inserted in the water to maintain turgidity. The leaves were replaced every three days until the parasitoid died. The replaced leaves were kept in other 350 mL plastic glasses, and after 15 days, all leaves were opened to collect the parasitoid pupae. The pupae were placed inside 10 mL plastic vials that were checked every day until the emergence of the parasitoids. The leaves were collected following the same process described in point 2.1. The rearing was maintained with mined coffee leaves that were collected weekly in the experimental field. All the leaves we collected were checked to assure that the coffee leaf miner larvae had not been preyed upon before using them in the parasitoid rearing, as predators break the surface of the mine to get to the larvae. Thus, we collected only intact mines. Medium-sized mines (about 1 cm diameter) were picked to maximize the occurrence of the first and second instars of the coffee leaf miner, which were assumed to be the preferred stages for the parasitoid’s oviposition [43].

2.3. Survival Experiments

To assess the effect of the plant resources (floral and extrafloral nectar) on *P. coffeae* survival, a non-choice experiment was performed in the laboratory. For *B. pilosa*, *G. parviflora*, and *V. curassavica*, the flowers were collected from plants naturally growing in the green areas of the Agriculture and Livestock Research Enterprise of Minas Gerais (EPAMIG), state of Minas Gerais, Brazil. The flowers of these plants were cut off from different plants and immediately transferred to a 350 mL plastic pot with their peduncles inserted in a 10 mL vial with water. This procedure was adopted as it was easier to handle than the entire plant, and there is evidence that this method does not alter the provision of nectar to natural enemies [44]. Flowers were replaced during the experiment when they became senescent (approximately every one or two days). In the case of *S. cernua*, in which the resource assessed was the extrafloral nectar, the experimental unit consisted of a clip cage (3 cm diameter) [15]. We placed one newly emerged *P. coffeae* female at approximately 10 h old, in separate plastic pots or clip cages (the experimental unit) containing one flower or extrafloral nectary of each plant inside. For the control group, one female of the same age

was kept inside a 350 mL plastic pot containing only water in cotton inside a 10 mL vial, and in the case of *S. cernua* the female was placed in a clip cage placed in a part of the plant without an extrafloral nectary.

The parasitoids were observed daily to assess their survival. For *B. pilosa* 20 *P. coffeae* were exposed to the floral nectar, and 22 were controls; for *G. parviflora* 22 parasitoids were exposed to the floral nectar, and 22 served as controls; for *V. curassavica* 22 *P. coffeae* were exposed to the floral nectar, and 22 were controls; for *S. cernua* 23 parasitoids fed on the extrafloral nectar and 23 serve as controls. For each plant species, the experiments were carried out simultaneously

2.4. Egg Load Experiment

Based on the results of the survival experiments (see below), we assessed whether feeding on extrafloral nectar from *S. cernua* would increase the egg load of *P. coffea* over time. We used the same experimental setup described for the survival experiments. However, in this experiment, we collected from the clip cages and dissected the parasitoids after a specific time measured in days. For two days, 11 *P. coffeae* were exposed to the extrafloral nectary and 12 were controls, for four days, 9 *P. coffeae* were exposed to the extrafloral nectary and 9 were controls, for six days, 9 *P. coffeae* were exposed to the extrafloral nectary and 8 were controls, for eight days, 5 *P. coffeae* were exposed to the extrafloral nectary and 3 were controls, and for ten days, 10 *P. coffeae* were exposed to the extrafloral nectary and 7 were controls. Each wasp was frozen for 3 min before being placed in an excavated plate with phosphate buffered saline solution to be dissected. Then, the ovaries were removed with fine needles, and the number of eggs was counted using a stereoscopic microscope.

2.5. Statistical Analysis

The survival of *P. coffeae* parasitoids when exposed to floral and extrafloral nectar were estimated by a Kaplan-Meier survival analysis. Each treatment was separately contrasted with its control. The effect of the extrafloral nectar of *S. cernua* on *P. coffeae* egg load and the parasitoid's age on their egg load was estimated by a Generalized Linear Model (GLM) with the Poisson distribution. In this model, the number of eggs (egg load) per day was used as the dependent variable, and the accessibility or not to extrafloral nectar and time, as well as their possible interactions, were used as independent variables. When some variable or interaction did not affect the dependent variable, it fit a new model. After reaching the final model, we assessed the significance of each variable by fitting an Analysis of Deviance (ANODEV) using a Chi-square test. The goodness of fit of the model was tested by a visual inspection of the model residuals. All the analyses were performed using the R software [45].

3. Results

Proacrias coffeae adult females survived longer when feeding on the floral nectar of *V. curassavica* (mean \pm SE 10.32 ± 2.23 days) than in the control group (3.41 ± 0.21 days) ($p < 0.0001$ Figure 1a). Similarly, *P. coffeae* that fed on extrafloral nectar from *S. cernua*, also lived longer (24.22 ± 2.78 days) than in the control (6.34 ± 1.36 days) ($p < 0.0001$; Figure 1b). The survival of parasitoids that were exposed to flowers of *G. parviflora* (4.50 ± 0.29 days) ($p = 0.29$; Figure 1c) and on *B. pilosa* (4.85 ± 0.50 days) ($p = 0.05$ Figure 1d) did not differ from their respective controls (*G. parviflora* control = 4.27 ± 0.26 days, *B. pilosa* control = 3.80 ± 0.32 days). Therefore, parasitoid survival was enhanced when females fed on floral nectar from *V. curassavica* and on extrafloral nectar of *S. cernua* (Figure 1).

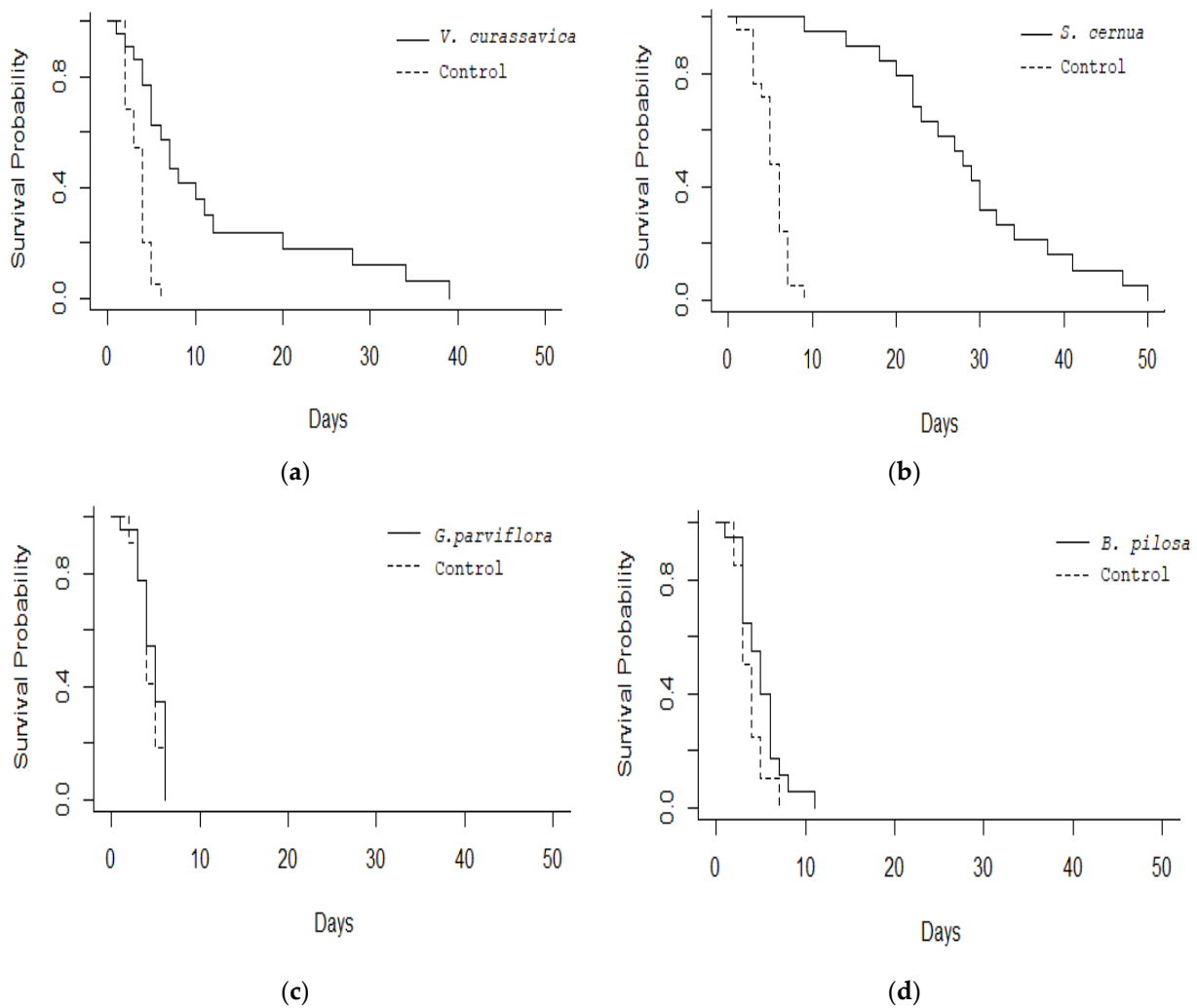


Figure 1. Kaplan-Meier estimates of survivorship functions of the coffee leaf miner parasitoid *Proacrias coffeae* exposed to the nectar of: (a) *Varronia curassavica* ($p < 0.0001$); (b) *Senna cernua* ($p < 0.0001$); (c) *Galinsoga parviflora* ($p = 0.29$); (d) *Bidens pilosa* ($p = 0.049$).

Due to the promising results found on the effects of *S. cernua* extrafloral nectar and its accessibility to *P. coffeae*, we also evaluated whether this plant could affect *P. coffeae* egg load. Overall, the egg load of *P. coffeae* females that had access to the extrafloral nectar of *S. cernua* increased from 4.32 ± 0.60 eggs/female to 5.74 ± 0.37 eggs/female during the experiment ($X_2 = 10.01$, d.f. = 1, $p = 0.0016$) (Figure 2).

Also, *P. coffeae* egg load increased with age, mostly when fed on *S. cernua* extrafloral nectar ($X_2 = 17.882$, d.f. = 4, $p = 0.001301$, Figure 3). However, regarding the parasitoid egg load, the age of *P. coffeae* females did not interact with *S. cernua* extrafloral nectar as a feeding resource, indicating that age and extrafloral nectar affected *P. coffeae* egg load independently ($X_2 = 4.0423$, d.f. = 4, $p = 0.400309$).

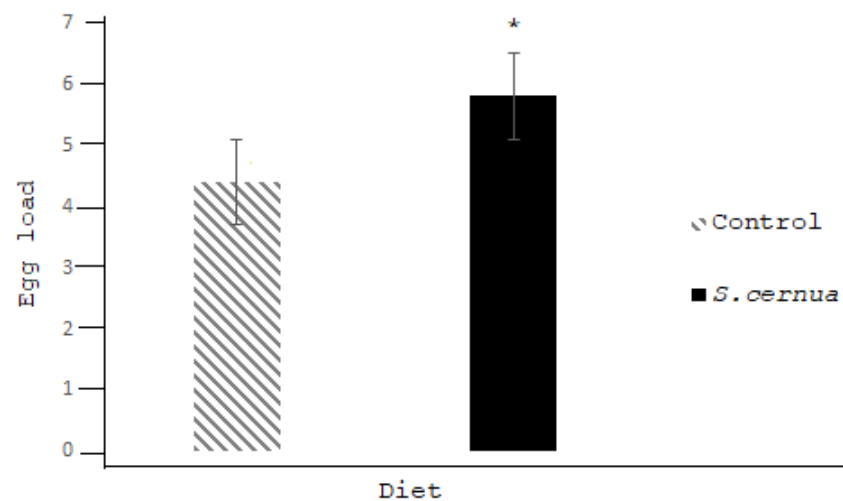


Figure 2. Mean of *Proacriascoffea* egg load (\pm SE) when fed on *Senna cernua* extrafloral nectar compared to the control (value with asterisk indicate significant differences at $p = 0.05$).

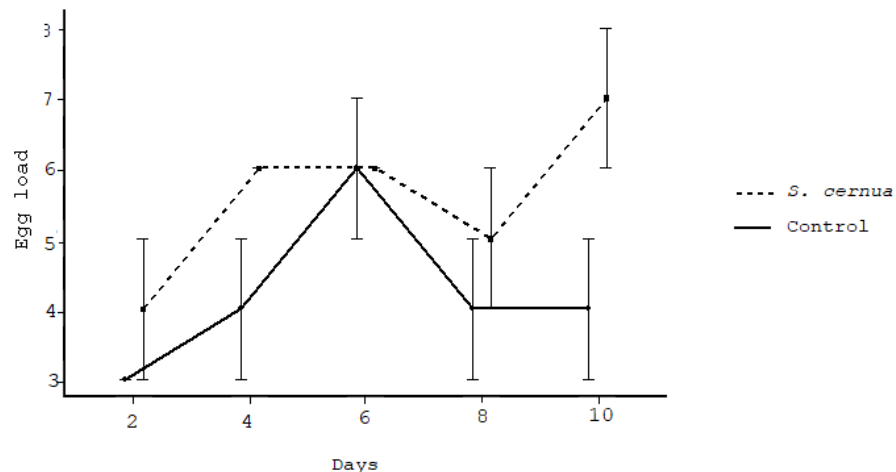


Figure 3. Mean of *P. coffeae* egg load (\pm SE) when fed on *S. cernua* extrafloral nectar compared to the control in different days after emergence.

4. Discussion

We found that *P. coffeae* feeds and survives longer on the nectar of *V. curassavica* and on the extrafloral nectar of *S. cernua*. We suggest that these results may be due to a combined effect on the parasitoid's capacity of accessing flower resources [37,39,46] and the quality of the nectar from these plants [7]. The accessibility and suitability of *S. cernua* extrafloral nectar also increased parasitoid reproduction, as we found an increase in parasitoid egg load when fed on this plant. Consequently, the increase in parasitoid fitness may positively impact females' retention in the crop and possibly their impact on the target pest [9,17]. On the other hand, our results indicate that nectar resources of *B. pilosa* and *G. parviflora* did not influence the conservation of *P. coffeae* for controlling the coffee leaf miner as they had no effect on parasitoid survival. Our results reinforce the need for critically evaluating the role of plant-provided food in conservation biological strategies instead of indiscriminately increasing plant diversity in agroecosystems [3,6].

The different results obtained regarding the plants we tested might be related to their morphological constraints. Stang et al. [47] found that whether the nectar holder increases in depth or decreases in width, the number of visitor species decreases. We looked at flowering plants with different flower morphologies and discovered that the parasitoids couldn't feed on any of the Asteraceae plants tested. Although various parasitoid families

have been observed on Asteraceae flowers, nectar accessibility has not been confirmed [48]. In general, *Bidens* sp. flowers could favor bigger visitors [49], and *Galinsoga* sp. and related Asteraceae have been observed to be more visited by flies, maybe due to their flowers' colors [50].

The quality of the nectar may also influence the effect of the feeding resources on the longevity of parasitoids. Sucrose-rich nectar seems to have a stronger effect on parasitoid survival than hexose-rich nectar [7]. Most Asteraceae species have hexose predominance in their sugar composition [51]. Therefore, Asteraceae nectar is expected to be a less suitable feeding resource for small parasitoids like *P. coffeae*, in terms of either accessibility or nectar nutritional quality.

Unlike the Asteraceae, feeding on the flowers of *V. curassavica* increased *P. coffeae* survival. The planthas been reported to be visited by several beneficial insects, such as pollinators, predators, and parasitoids [52]. It has the capacity to flower through the entire year with an increment in the warmer months [37,53], which makes them a good alternative to offering feeding resources to natural enemies. Therefore, this plant could be used to improve biological control services as well as other ecosystem services such as pollination, which is desirable for biodiversity and ecosystem services in tropical regions, such as Brazil [54,55]. The floral morphology of this plant allows small parasitoids to access the nectar, given that they have wide corollas. The mouth parts of parasitoids are not specialized to feed on the floral nectar of flowers with long corollas and benefit more from exposed nectar sources, such as open and short corollas, as observed in *V. curassavica* [44,56,57].

In the case of extrafloral nectar, the parasitoids do not deal with morphological constraints since the nectar is totally exposed. Rezende [15] showed that *P. coffeae* can feed on *Inga* sp. extrafloral nectar, which increases its survival as well as that of other coffee leaf miner parasitoids. Extrafloral nectar presents other benefits such as temporal availability and the potential for selective use by lepidopteran parasitic wasps since their concentration constrains the nectar uptake for lepidopteran insects [56,58].

The increased longevity of *P. coffeae* when fed nectar from *V. curassavica* and extrafloral nectar from *S. cernua* may benefit parasitism by giving parasitoids more time to forage for hosts while maturing their eggs. We confirmed that *P. coffeae* females emerge with a few mature eggs, and their egg load increases over time since they are synovigenic parasitoids [13]. Adult synovigenic parasitoids allocate the resources for egg production from teneral reserves (acquired during larval feeding) and dietary components [59]. Synovigenic parasitoids acquire nutrients that can be allocated for maintenance or oogenesis and egg maturation, and scarcity of food can lead to a tradeoff between those two processes [8]. In terms of conservation biological control, parasitoids must deal with the decision of foraging for hosts or food. In this sense, the presence of a quality food source nearby the host can help solve this issue and allow the parasitoids to remain in the agroecosystem for longer periods [60]. Here we found that *P. coffeae* produced a higher number of mature eggs when fed on *S. cernua* extrafloral nectar, suggesting that the energy ingested by feeding on the nectar of this plant could be converted to oogenesis. Therefore, *S. cernua* can be a suitable option to diversify coffee crops by rewarding *P. coffeae* in terms of feeding and reproduction [30].

We suggest an initial screening of the plants to be considered in future experiments on *P. coffeae* fitness and similar parasitoids based on their floral morphology (particularly the position of the nectaries in flowering plants). Our findings show that *V. curassavica* and *S. cernua* have the potential to provide nutritional resources to the parasitoid *P. coffeae*, thereby increasing their fitness by increasing survival in the case of both plants and parasitoid egg loads in the case of *S. cernua* extrafloral nectar. It is possible that the same occurs for *V. curassavica*, but for logistical reasons, we did not test this plant in our study. Studies on *S. cernua* attractiveness need to be performed to assess their potential to attract the parasitoid in the field. This finding leaves a lead on the kind of plants that can be used when aiming to

control the coffee leaf miner in tropical agroecosystems. We suggest that native flowering plants with exposed nectaries and/or extrafloral nectaries should be prioritized.

Author Contributions: Conceptualization, C.C.-A. and M.V.; methodology, C.C.-A. and M.V.; validation, P.H.B.T.; formal analysis, P.H.B.T. and C.C.-A.; investigation, C.C.-A. and G.M.P.; resources, M.V.; data curation, C.C.-A.; writing—original draft preparation, C.C.-A.; writing—review and editing, P.H.B.T., A.S.S. and M.V.; visualization, C.C.-A. and P.H.B.T.; supervision, M.V.; project administration, M.V.; funding acquisition, M.V. All authors have read and agreed to the published version of the manuscript.

Funding: This study was financed by ‘Conselho Nacional de Desenvolvimento Científico e Tecnológico’ (CNPq, 312784/2021-0), ‘Fundação de Amparo à Pesquisa de Minas Gerais’ (FAPEMIG, CAG-PPM-00270/18), ‘Coordenação de Aperfeiçoamento de Pessoal de Nível Superior-Brasil’ (CAPES)-Finance Code 001 and Consórcio Brasileiro de Pesquisa e Desenvolvimento do Café (CBP&D-Café, 10.18.20.049.00.04).

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The data is available upon request from the corresponding author.

Acknowledgments: The authors would like to thank Valmir Costa (Instituto Biológico de São Paulo) for his help with the parasitoid’s identification. We are also grateful with Angelo Pallini (Universidade Federal de Viçosa) for his support in providing space in his laboratory during the pandemic situation and with Paulo Henrique Rezende for the training on the parasitoid’s dissection.

Conflicts of Interest: The authors declare no conflict of interest. The company of M.V. (Agriculture and Livestock Research Enterprise of Minas Gerais) is a government research company of Minas Gerais state. This company has a partnership with the Federal University of Viçosa (UFV) to receive students and develop research. This paper is the result of C.C.-A. master at UFV, under the M.V. guidance.

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