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Original Article

Trap-nesting biology of an ectoparasitoid spider wasp, *Auplopus subaurarius* (Hymenoptera: Pompilidae): the importance of wooded environments for niche generalist species

Biologia de nidificação em ninhos-armadilha da vespa ectoparasitoide de aranhas *Auplopus subaurarius* (Hymenoptera: Pompilidae): a importância de ambientes arborizados para espécies generalistas de nicho

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Abstract

The insect group is one of the most diverse on the planet and due to habitat degradation, many of these species are becoming extinct, leaving a lack of information on the basic biology of each one. In this study, previously unseen information about nesting biology is revealed in *Auplopus subaurarius* trap nests. This is a solitary ectoparasitoid spider wasp that nests in preexisting cavities. We used a trap-nesting methodology to sample *A. subaurarius* in two different sampling periods (2017/2018 and 2020/2021) in three types of environment (forest, grassland and *Eucalyptus* plantation). In our study, the *A. subaurarius* nest building was more frequent during the hottest months of the year (November to March), with its highest abundance found within natural forest areas and in *Eucalyptus* plantation than in grassland areas. In addition, the species had two development times: a short one (three months) and a delayed one (up to one year). Moreover, females were larger than males (weight and size) and the species' sex ratio had a tendency toward female production. *Auplopus subaurarius* presented seven natural enemy species: *Ceyxia longispina*, *Caenochrysis crotonis*, *Photochryptus* sp.1, *Photochryptus* sp.2, *Messatoporus* sp., *Ephuta icema* and *Sphaeropthalma* sp. We emphasize the importance of wooded environments to maintain the *A. subaurarius* populations and their associated interactors, both spiders and natural enemies, as these environments can provide better life conditions than grassland areas. Furthermore, other solitary wasps that may have the same lifestyle of *A. subaurarius* can also be improved by natural forest conservation and by good silviculture plantation planning, which should consider ecological aspects of Atlantic Forest landscapes.

Keywords: *Araucaria* forest, *Eucalyptus*, trap-nest, solitary, sex ratio.

Resumo

O grupo dos insetos é um dos mais diversos do planeta e devido à degradação dos habitats, muitas dessas espécies estão sendo extintas, deixando uma carência de informações sobre a biologia básica de cada uma. Neste estudo, informações inéditas sobre a biologia de nidificação em ninhos-armadilha de *Auplopus subaurarius* são reveladas. Essa espécie trata-se de uma vespa solitária ectoparasitóide de aranhas, que nidifica em cavidades preexistentes. Utilizamos a metodologia de ninhos-armadilha para amostrar *A. subaurarius* em dois períodos amostrais diferentes (2017/2018 e 2020/2021), em três tipos de ambientes (floresta, campo e plantação de *Eucalyptus*). Em nosso estudo, a nidificação de *A. subaurarius* foi mais frequente nos meses mais quentes do ano (Novembro a Março), com maior abundância encontrada em áreas de floresta nativa e em plantações de *Eucalyptus* comparados à áreas de campo. Além disso, a espécie apresentou dois tempos de desenvolvimento, um curto (três meses) e um longo (até um ano). Além disso, as fêmeas foram maiores que os machos (peso e tamanho) e a razão sexual da espécie apresentou tendência à produção de fêmeas. *Auplopus subaurarius* apresentou sete espécies de inimigos naturais: *Ceyxia longispina*, *Caenochrysis crotonis*, *Photochryptus* sp.1, *Photochryptus* sp.2, *Messatoporus* sp., *Ephuta icema* e *Sphaeropthalma* sp. Ressaltamos a importância de ambientes arborizados para manutenção das populações de *A. subaurarius* e seus interagentes associados, tanto aranhas quanto inimigos naturais, uma vez que estes ambientes podem apresentar melhores condições de vida comparados à áreas campestres. Além disso, outras vespas solitárias

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que podem ter o mesmo estilo de vida de *A. subaurarius*, também podem ser afetadas positivamente pela conservação das florestas naturais e por um bom planejamento de plantações de silvicultura, as quais devem considerar os aspectos ecológicos das paisagens da Mata Atlântica.

Palavras-chave: floresta de Araucárias, *Eucalyptus*, ninho-armadilha, solitária, razão sexual.

1. Introduction

Insects are one of the most biodiverse groups in the animal kingdom and can provide important ecosystem services (Noriega et al., 2018). It is estimated that the contribution of insects to the worldwide economy is billions of dollars per year (Losey and Vaughan, 2006; IPBES, 2016). Due to this, most studies that aimed to understand ecosystem services are carried out with insects, in which most research has been done in the Hymenoptera order, one of the most diverse groups in insects (Noriega et al., 2018). Despite this, the studies often focus on pollination services provided by bees (Noriega et al., 2018), ignoring species that have more generalist lifestyles and can provide other ecosystem services, such as wasp species. Wasps are carnivores (controlling the population of other arthropods), playing different roles in the ecosystem, by predation as well as parasitoid interactions (Brock et al., 2021).

Despite this ecosystem and economic importance, insects are one of the most affected by habitat degradation, especially in regions that are more populated by humans, where the need to use natural areas for profit is greater (Sánchez-Bayo and Wyckhuys, 2019). In Brazil, an example of these environments is the Atlantic Forest biome, where the landscape has been altered, showing significant fragmentation and loss of habitat (Ribeiro et al., 2009; Rezende et al., 2018). In this biome, about 60% of flora and fauna and 25% of endemic species are threatened (Paglia et al., 2008). Owing to this, many species are lost before being described or studied in more depth; mainly species that are less targeted by conservation policies, such as wasp species.

Much remains to be discovered about wasp species, such as their natural history, behavior, phylogeny, evolution and importance for the maintenance and regulation of ecosystem processes (Brock et al., 2021). For instance, the Pompilidae family, also called spider wasps, is a monophyletic wasp family, that provides their offspring with spiders as a food source (Iwata, 1976; Kurczewski, 2010; Kurczewski and Edwards, 2012; Kurczewski et al., 2017; Kurczewski and West, 2022). Despite this monophyly, this family still has many unresolved questions about its evolution and position in the phylogenetic tree (Shimizu et al., 2010; Rodriguez et al., 2016). This is mainly due to a great variation within these wasps, regarding their natural history, behavior and the similarity in corporal traits among species (Waichert et al., 2015; Kurczewski et al., 2017; Kurczewski and West, 2022).

The Pompilidae family has about 4,855 described species distributed into 120 genera, with a cosmopolitan distribution, and the highest diversity in the tropical regions (Fernández, 2000; Pitts et al., 2006). Approximately 63 genera and 946 species were described for the Neotropical region (Fernández, 2000). In Brazil, many species occur in the Atlantic Forest biome, and therefore, they are also at risk of disappearing due to anthropic activities (Colombo and Joly, 2010). Much information about the biology of these species may be lost before we have time to know them, which may affect future studies aimed at understanding the evolution and phylogeny of this group. Therefore, studies that aim to gather information not yet seen on the basic ecology and natural history of these species may be fundamental to provide stronger bases for future studies.

One of the genera of Pompilidae that lacks fundamental information is *Auplopus* Spinola, 1841 (Quijano-Cuervo et al., 2021), which has about 119 species in the Neotropical region (Fernández, 2000). The species of this genus vary in their behavior, as they are solitary, communal or even parasocial, which arouses interest among scientists to understand the evolution of social systems (Evans and Shimizu, 1996; Wcislo et al., 1988; Shimizu et al., 2010; Barthélémy and Pitts, 2012). Furthermore, the *Auplopus* species can also be classified regarding their hunting ecology as ectoparasitoids of spiders, where the female provides only one spider per nest cell, on which it lays an egg that will feed on this spider host (Shimizu et al., 2010; Rodriguez et al., 2016). This type of behavior makes these species very useful to be used as bioindicators, because generally parasitoid species that are at a higher trophic level are more sensitive to environmental changes because they are highly dependent on the occurrence of their hosts for their larval development (Oliveira and Gonçalves, 2017; Tylianakis and Morris, 2017).

Despite the environmental importance of *Auplopus* species, many of them have not yet been studied for their basic ecological aspects, which prevents the development of more applied studies (Quijano-Cuervo et al., 2021). One of these species is *Auplopus subaurarius* Dreisbach, 1963, a solitary wasp, which builds their nests in preexisting cavities, where the females construct a varied number of brood cells, which have a barrel shape and are made of clay (Buschini et al., 2007; Nether et al., 2019; Buggenhagen, 2016). *Auplopus subaurarius* has been found nesting in the *Araucaria* Forest, one of the phytophysiognomies of the Atlantic Forest biome (Buschini et al., 2007; Buschini and Woiski, 2008; Iantas et al., 2017; Cambra et al., 2017, 2021). These forests can be found in the southern region of Brazil and are characterized by the presence of the conifer *Araucaria angustifolia* (Bertol.) Kuntze, which makes a specific canopy cover and can be recognized very easily. The *Araucaria* Forest, as well as many other phytophysionomies of the Atlantic Forest, has been extremely explored, and few fragments remain, which are at constant risk of disappearing as the *Araucaria angustifolia* is on the IUCN Red List of Threatened Species (Thomas, 2013).

Considering the importance of wasps, such as *A. subaurarius*, providing important ecosystem functions, the lack of basic information about their nesting ecology, and the risk of disappearance of their natural habitats, this study intends to bring to light new knowledge about the *A. subaurarius*, revealing new aspects about its nesting ecology, differences between females and males (weight, intertegular distance and head width), their development time, sex ratio and their natural enemies. To do this, we developed a sampling of A. subaurarius using the trap-nest methodology in different environments of the *Araucaria* forest phytophysiognomy in two different sampling periods between 2017/2018 and 2020/2021.

Considering previous studies carried out with other *Auplopus* species, we expect that the *A. subaurarius*: (1) is niche generalist in habitat type to build their nests, nesting both in open and wooded areas; (2) females of the species are larger than males and the sexual ratio will be 1:1; (3) is a multivoltine species; and (4) will be parasitized by natural enemies.

2. Material and Methods

2.1. Study area

The study had two different sampling periods. The first sample was made from August 2017 to July 2018 and the second sample was made from September 2020 to March 2021. Regarding the 2017/2018 data, samples were taken in two forested areas and two grassland areas. In each area, six points were sampled, totaling 24 sample points. To obtain the 2020/2021 data, the samples were taken in three different environmental areas: A *Eucalyptus* plantation; a forested area; and a grassland area. In each area, six points were sampled, totaling18 sample points. All samples were taken in private rural properties of the Guarapuava municipality, Paraná, Brazil (Figure 1).

The *Eucalyptus* area contained only this plant species, which was planted at periodic distances from each other, with no understory. The forest fragments are part of the phytophysiognomy of the Atlantic Forest called the Mixed Ombrophilous Forest, also known as the *Araucaria* Forest, which is characterized by an association between leafy species and the conifer *Araucaria angustifolia* that stands out among the crowns of other trees. Grasslands were areas without forest, usually used for animal husbandry. According to the Köppen classification, the Guarapuava climate is subtropical humid mesothermal (Cfb), in which the hottest period is from September to March (temperatures at about 23.5 °C) and the cold season extends from May to August (temperatures about 12.8 °C) (Kottek et al., 2006; IAPAR, 2019).

2.2. Sample design

To sample *A. subaurarius*, the trap-nest technique was used, which consists of providing artificial cavities for these insects to build their nests (Staab et al., 2018). These

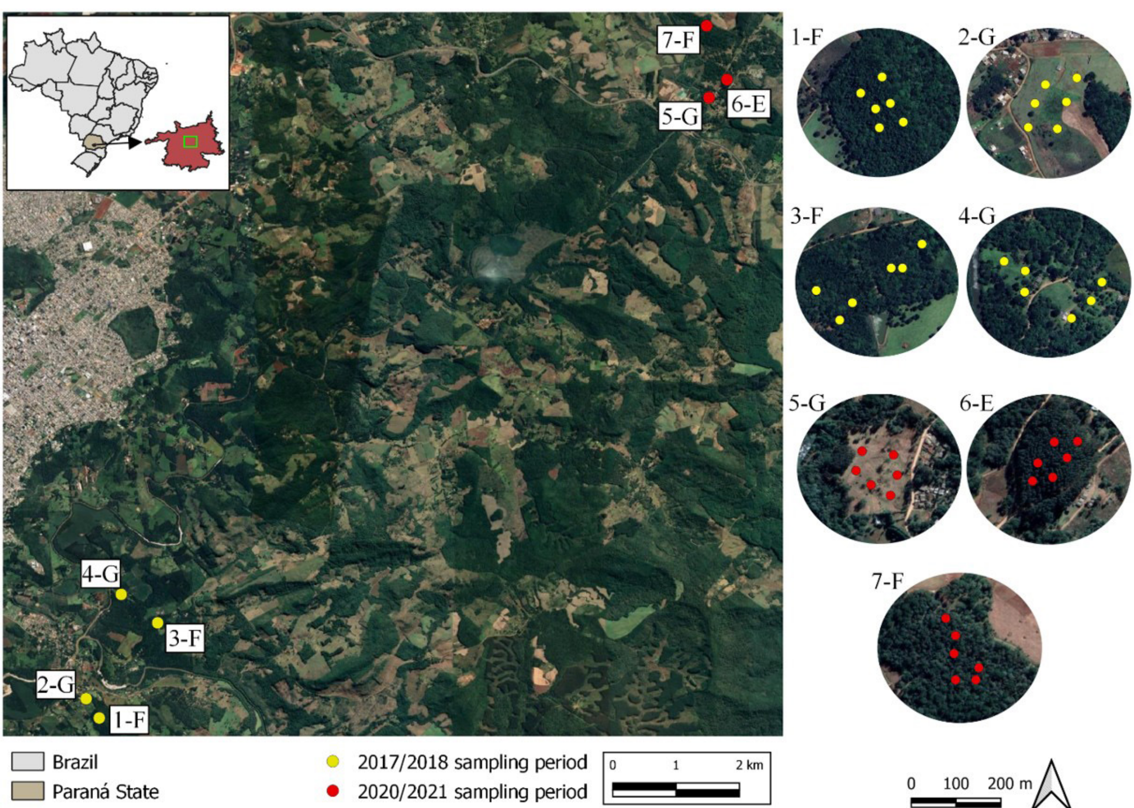

Figure 1. Study site located at Guarapuava municipality, Paraná State, Brazil, where *A. subaurarius* was collected. Yellow dots refer to the 2017/2018 sampling period and red dots refer to the 2020/2021 sampling period. F= Forested areas, G= Grassland areas, E= *Eucalyptus* area.

traps were made of wood and bamboo. The wooden ones were 2 cm (width), 2 cm (height) and 12 cm (length) and have cavities of 0.5, 0.7, 1, 1.3 cm of diameter and 8 cm of inner length. Bamboo traps varied in length and diameter, as their normalization was not possible due to their great diversity of sizes.

A wooden stake containing a block with 16 wooden trap-nests (four of each diameter) and 16 bamboo trap-nests was placed in each sample point, which were separated by 50 m from each other. Thus, in each sample point, there were 32 trap-nests, totaling 1,334 nests available across two sampling periods. The nests were monitored biweekly and when they were finalized, they were collected and replaced with other nests with the same diameter or similar size when the nests were made out of bamboo. After that, the collected nests were taken to the Bees and Wasps Biology and Ecology Lab (LABEVESP), Department of Biology (DEBIO), at the *Universidade Estadual do Centro-Oeste* - UNICENTRO, Guarapuava, Paraná, Brazil, until the adults emerged. After they emerged, the individuals were killed with ethyl acetate and identified. Those belonging to *A. subaurarius* were separated for study purposes.

2.3. Description of nest architecture, adult size, development time and sex ratio

To describe the nests and their contents, measurements of the brood cells (width and length) were taken, using a digital pachymeter. To measure the weight of individuals (made just after the adult emergence), a precision scale with four decimal places was used (Bel brand). We also took measurements of intertegular length and head diameter, using a stereomicroscope (Leica MZ6). Moreover, we also provided a visual description of the *A. subaurarius* nests and cocoons.

The wasp's development time was calculated as the number of days elapsed from the date of collection to the emergence of the adult. The number of adult generations was calculated from the month in which the species began to build its nests until the beginning of diapause, when nesting ceased. The sex ratio was measured using the number of females and males that emerged.

Regarding the natural enemies of *A. subaurarius*, we identified the interaction between each other. We also used the nests from which these two species emerged. As in *A. subaurarius* nests, many brood cells are built and just some of them are parasitized, natural enemies and hosts (A. subaurarius) emerged from the same nest, which enabled us to associate these two species.

2.4. Statistical analysis

All collected data were tested using the Shapiro-Wilk normality test. We used the binomial test and the Mann-Whitney test to compare *A. subaurarius* data. The Binomial test compares the observed frequency of two binary variables, where the expected proportion of each one is 0.5, and analyzes the probability of the success of one of the variables being more observed compared to the other. The Mann-Whitney test is a non-parametric test applied to two independent samples, indicated when the numerical variable does not present a normal distribution and/or when there is no homogeneity of variances.

We used the binomial test to assess the difference in *A. subaurarius* abundance between environments monthly and evaluated the expected sex ratio deviation of 1:1. To assess the statistical difference on abundance between environments in each year, the brood cells length and width between nest diameters and the size between females and males of *A. subaurarius*, we used the Mann-Whitney test. All the tests were carried out using the 'stats' package from RDocumentation, RStudio version 4.1.3 (R Core Team, 2022).

3. Results

In our study, *A. subaurarius* built 115 nests. Among these nests, 98 were built in the first sampling period (2017/2018) and 17 nests were built in the second sampling period (2020/2021). Among all the nests, 292 brood cells were built (average three per nest), 165 (56.5%) results in adult *A.subaurarius* emerged and 127 (43.5%) resulted in deaths.

Auplopus subaurarius was found in all the environmental types studied and nidified from September 2017 to July 2018 and from November 2020 to February 2021. For the first sampling period, this wasp was more abundant in the forested areas (199 built cells), followed by grassland areas (37 built cells), while the second sampling period had the same abundance in *Eucalyptus* areas (12 built cells) and forested areas (12 built cells) and did not nest in grassland areas. Unfortunately, the information of the sampling area of 14 nests were lost (32 built cells) (Figure 2, Table S1).

3.1. Nest architecture

Auplopus subaurarius presented a higher rate of nidification in the wood trap nests (171 built cells) than the bamboo trap nests (121 built cells). The diameters that were more used by the species were 1.3 cm, followed by 0.7 cm, 0.5 cm and 1 cm (Table S2). The nest architecture (brood cell size and shape and way to build cells) varied according to the nest diameter as in the nest with a lower diameter, the brood cells were built linearly in one row (nests with 0.5 cm to 0.7 cm of diameter), while in larger diameters, *A. subaurarius* built two rows of brood cells (Figure 3, Figure S1 and S2).

The cell number inside the nests varied from 1 to 22 cells per nest. There was no clay partition between each cell. The brood cells had a barrel shape and all of them were built out of little clay balls, making a pale brown cell (Figure 3, Figure S1 and S2). The individual cocoons stayed inside the cells and had a whitish color made with a material similar to silk paper, which was adhered to the posterior part of the brood cell (Figure 3, Figure S1 and S2). In the nest entrance, these wasps built a closure plug, made with clay, which is broken when the adult offspring emerged, and in some nests, the wasps filled the nest entrance with dry plant material (nests with 1 cm to 1.3 cm of diameter) (Figure 3, Figure S1 and S2). The average brood cell size was 1.26 cm long and 0.65 cm wide (Table 1). Furthermore, males and females were oviposited within the same nest and the position of each one within the nest was random.

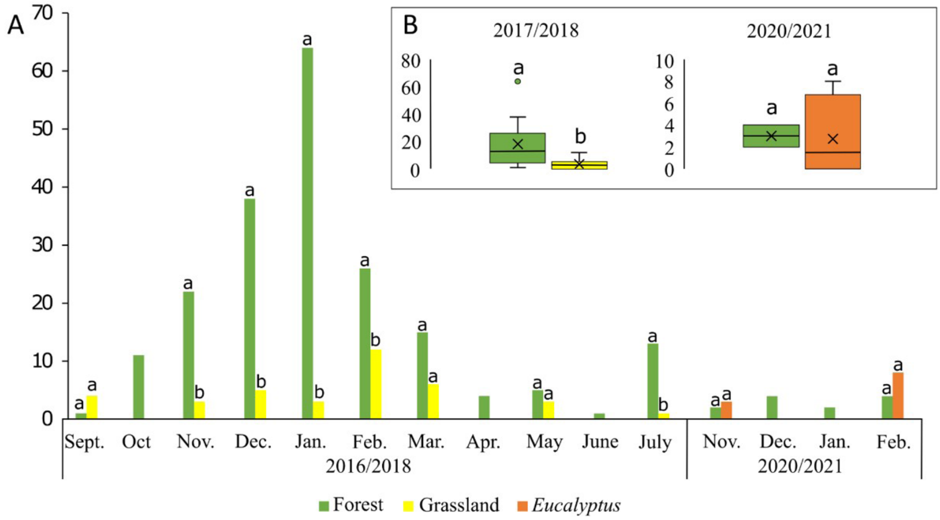

Figure 2. Abundance of *A. subaurarius* (considering the number of cells with both *A. subaurarius* and natural enemies) in 2017/2018 and 2020/2021 for each sample environment. Green bar: Forest, yellow bar: grassland areas and orange bar: *Eucalyptus* plantation. A: Pairwise comparisons between environments in each month by binomial test; B: Total comparison between each environment for each year by Mann-Whitney test (x indicates mean and line indicate median). Different letters above the bars indicate significant differences. For the significance test values, see Table S1 in the Supplementary Material.

Figure 3. Nest architecture of *A. subaurarius*. 1- Cocoon inside of brood cell; 2- Dry plant materials in nest entrance; 3- Brood cell; 4- Another dry plant material type in the nest entrance. For more nest architecture images, please see the Supplementary Material.

Table 1. Nest brood cells measures of *A. subaurarius*. Different superscript letters indicate the significant differences (for significance values, see Table S2 of the Supplementary Material). $\bar{x}$: mean.

Nest diameter	Brood cell length (cm)	Brood cell width (cm)
0.5	$\bar{x} = 1.10 \pm 0.12^{a}$	$\bar{x} = 0.45 \pm 0.1^{a}$
0.7	$\bar{x} = 1.20 \pm 0.08^{a}$	$\bar{x} = 0.71 \pm 0.01^{b}$
1	$\bar{x} = 1.38 \pm 0.01^{a}$	$\bar{x} = 0.76 \pm 0.01^{b}$
1.3	$\bar{x} = 1.38 \pm 0.04^{b}$	$\bar{x} = 0.83 \pm 0.04^{c}$
Total	$\bar{x} = 1.26 \pm 0.15$	$\bar{x} = 0.65 \pm 0.13$

3.2. Adult size, development time and sex ratio

The females of *A. subaurarius* were significantly higher than males in weights, intertegular distance and head diameter (Table 2, Figure S3). Regarding the development time, *A. subaurarius* presented two different times: one was a short development time (it lasted between 30 to 60 days) and one was a delayed development time, in which individuals entered diapause and emerged only after passing through the winter (with the longest recorded time of 416 days). Considering the short development time of 30 days, *A. subaurarius* may have had up to 10 generations in 2017/2018 and up to 3 generations in 2020/2021, which characterizes this species as multivoltine (Figure 4).

Table 2. Comparisons between females and males of *A. subaurarius* with respective p values (bold values are significant). $\bar{x}$: mean.

	Female	Male	Mann-Whitney test (*U*)	*p*
Weight	$\bar{x} = 0.026$	$\bar{x} = 0.012$	4615.5	**3.4E-17**
Intertegular distance (mm)	$\bar{x} = 1.687$	$\bar{x} = 1.261$	6819	**5.4E-23**
Development time (days)	$\bar{x} = 135$	$\bar{x} = 140$	3191.5	0.9320
Direct development (days)	$\bar{x} = 25$	$\bar{x} = 25$	1168	0.8410
Delayed development (days)	$\bar{x} = 303$	$\bar{x} = 302$	541.5	0.8500

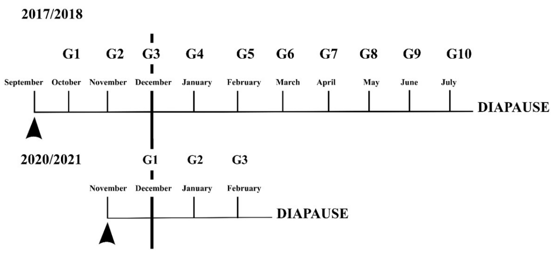

Figure 4. Development time and possible number of generations of *A. subaurarius* during two sampling periods. The arrow indicates the first nesting record. The number of generations was calculated considering a development time of thirty days.

We were able to identify the sex of 175 individuals, in which 105 were female and 70 were male. They differed significantly from the expected sex ratio of 1:1, indicating that *A. subaurarius* had a tendency to produce females. When we calculated the sex ratio for the two development times separately, we found the same result for direct development (52 females and 29 males), but there was no difference in the delayed development from the expected proportion 1:1 (39 females and 26 males). We also saw a significant tendency to produce females in the first sampling period, while in the second sampling period there was no different of sex ratio from 1:1 (Table 3).

Table 3. Binomial test for *A. subaurarius* sex ratio (bold values are significant).

	Female	Male	*p*
Total*	105	70	**0.0090**
Direct development	52	29	**0.0190**
Delayed development	39	26	0.1360
First sampling period (2017/2018)	91	60	**0.0143**
Second sampling period (2020/2021)	14	10	0.5413

*This value represents all the individuals who were sexed, regardless of whether they had their time of development measured or not.

3.3. Mortality and natural enemies

The *A. subaurarius* mortalities were: 11 dead eggs (3.8%), 19 dead larvae (6.5%), 2 dead pupae (0.6%), 66 dead adults (22.6%), all by unknown causes and 29 more dead adults by natural enemies (10%) (Table 4). The natural enemies were found in just the first sampling period (2017/2018), therefore, no one was found on the *Eucalyptus* plantation. The forest was the habitat that was more used by natural enemies to parasitize *A. subaurarius* nests and just two were found in the grassland areas (Table 4).

Table 4. Abundance of natural enemies that parasitize *A. subaurarius* in each environment.

Natural enemies		Forest	Grassland	Total
Chalcididae				
	Ceyxia longispina Andrade and Tavares, 2009	0	2	2
Chrysididae				
	Caenochrysis crotonis (Ducke, 1906)	2	8	10
Ichneumonidae				
	Photochryptus sp.1	3	0	3
	Photochryptus sp.2	10	0	10
	Messatoporus sp.	1	0	1
Mutillidae				
	Ephuta icema Casal, 1969	1	0	1
	Sphaeropthalma sp.	2	0	2

The natural enemy species was found only in the first sampling period (2017/2018).

4. Discussion

The nidification of *A. subaurarius* was more frequent in the hottest months of the years. Moreover, the species nested in all studied environments, which was a niche generalist species in the choice of habitat. Despite *A. subaurarius* being niche generalist, concerning the habitat type, we saw that higher nidification was in forests in the first sampling period, which may mean that there may be a preference for this environment. The explanation for that can be the availability of resources that are often higher in native forest areas (Fornoff et al., 2021). Many other solitary wasp species that behave similarly use the forests to obtain resources as shelters and/or food, thus being able to survival and reproduce (Buschini et al., 2006; Buschini and Buss, 2014; Fornoff et al., 2021).

Auplopus subaurarius is not the only *Auplopus* species that occurs in *Araucaria* forests. Other examples are

Auplopus tarsatus (Smith, 1873) and *Auplopus rufipes* (Banks, 1946) (Nether et al., 2019). In a study carried out by Buschini et al. (2007), the authors found five different morphotypes of *Auplopus* in this region, and despite the fact that the specimens were not identified at a species level, these results show us the importance of this phytophysiognomy to the community of spider wasp maintenance. Regarding *A. subaurarius*, we observed that in the first sampling period, replacing forested areas by grassland areas decreased their abundance, while in the second sampling period, their abundance was the same in the forested areas and *Eucalyptus* plantation. Caution should be taken when drawing conclusions about the effect of the *Eucalyptus* areas due to the smaller sampling effort that we had in that area as the collections were made focusing on other purposes than the ecology of *A. subaurarius*, which could also explain the absence of natural enemies of *A. subaurarius* in this area. Although *Eucalyptus* areas are not a natural vegetation cover, they can provide resources such as shelter due to the greater production of leaf litter and present greater vegetational complexity for web building to spider species, compared to grassland areas (Baldissera et al., 2008; Rodrigues et al., 2010). Moreover, grassland areas are prone to higher light intensity, rainfall, wind, and greater visibility of predators than areas of natural forest and *Eucalyptus* plantations (Rodrigues et al., 2010), which can negatively affect both the abundance of *A. subaurarius* and its host spiders. Therefore, conserving natural forested areas and developing good silviculture plantation planning in the Atlantic Forest may increase these arthropod species diversity and their associated ecosystem services.

The spiders used by *A. subaurarius* can significantly affect their abundance, as spiders are the trophic resource used by *A. subaurarius* larvae to complete their development. Previous studies show that the genus *Auplopus* is quite polyphagous in the host selection, using several spider families as food for their offspring, such as Gnaphosidae, Thomisidae, Salticidae, Clubionidae, Anyphaenidae, Lycosidae, Araneidae (Shimizu et al., 2010; Kurczewski, 2010; Kurczewski and Edwards, 2012; Kurczewski et al., 2017; Kurczewski and West, 2022). This non-selective preference for their host is related to their niche generalist behavior, nesting in several environments where spiders are more diverse (Kurczewski and Edwards, 2012), such as wooded areas (natural forests and *Eucalyptus* plantation). Despite polyphagia, there is a positive size relationship between Pompilidae spider wasps and host spiders as larger Pompilidae species tend to parasitize larger family spiders, while smaller wasps, such as *Auplopus* genera, tend to parasitize spider families with smaller sizes (Kurczewski and Edwards, 2012; Kurczewski et al., 2017; Kurczewski and West, 2022).

Most of the nests used for oviposition of *A. subaurarius* were wooden trap nests, which had a varying number of cells, all built out of clay. This nest architecture was similar to observations of other studies on *Auplopus* (Buschini et al., 2007; Zanette et al., 2004; Gonzaga and Vasconcellos-Neto, 2006). Many factors can influence the cavity choice for wasp nidification, such as rain protection, which has already been observed by studies that show that the protection of traps against rain increases wasp nidification (Taki et al., 2008). Another factor may be a specialization that occurs in the species regarding the nest diameter (Budrienė and Budrys, 2005), where some species choose their nests according to their body sizes or host sizes (Kurczewski et al., 2017; Lima et al., 2020; Kurczewski and West, 2022). In our study, the type of nest (bamboo or wood) can also influence nesting. Wooden trap nests are thicker, which can protect the nest from temperature fluctuations, compared to thinner bamboo nests. Guarapuava, where the collections were carried out, is a municipality with a severe winter that experiences negative temperatures and frequent frosts (IAPAR, 2019). Therefore, wooden nests may be chosen more often than bamboo nests.

An interesting point about nest architecture of *A. subaurarius* is that some females filled in the nest entrance with various dry pieces of wood and in some nests, they built a closure plug (Figure 3, Figure S1 and S2). To the best of our knowledge, there have been no records about this behavior in this species. The purpose of this behavior seems to be related to nest protection against natural enemies. Thus, considering that *A. subaurarius* used the plant material in the nest entrance to avoid natural enemies, future studies could analyze if there is any difference in the parasitism rate between nests that have these plant materials and those without this protection. Many other studies already found similar characteristics in other solitary wasps. In a study carried out by Krombein and Burks (1967), the author concluded that the empty cells located at the nest entrance, between the first brood cell and nest closure, were built to avoid natural enemy attacks. Another study, carried out by Staab et al. (2014), showed another peculiar form used by wasps to avoid attacks by natural enemies, where the female wasp filled the nest entrance with many dead ants, which could chemically disguise their nests. Finally, another example is shown by Deus et al. (2021), where the authors found a reinforcement of nest closure made out of plant material and resin in nests of other solitary wasps, which may also be related with nest protection. From these examples, we can assume that the behavior observed in *A. subaurarius* may also be a way to protect their nests against natural enemies.

Inside the nests, females and males were randomly oviposited both in the innermost cells and outermost cells. Despite this, the females were larger in size and weight and there was a tendency for female production in the first sampling period, while in the second sampling period there was no difference from that expected of a proportion sex ratio of 1:1. The main factor that may influence the sex ratio of solitary wasps is the nest diameter, where the smaller diameter nests may not have females, which are usually larger than males (O'Neill, 2001). Besides that, Buschini et al. (2007), who studied different *Auplopus* species, rules out this possibility due to the presence of females in smaller diameter artificial nests, which also happened in the present study. Sex determination may also be a function of host size as *A. subaurarius* females are bigger than males and the size of Pompilidae adult wasp's resulting from a spider host depends on the amount of food stocked for its development (spider size) (Kurczewski and Edwards, 2012), *A. subaurarius* may prefer oviposit females in bigger spider hosts and males in smaller ones. Moreover, another factor that may affect the tendency to produce more females than males is the availability of food (Polidori et al., 2011). Previous studies have already shown that there is a high sex ratio variation every year, and the possible explanation for this is food availability, where years with more amount of trophic resource presents more females (Kümmerli and Keller, 2011). Therefore, our first sampling period may have only shown one year where food availability was higher and the sex ratio tended toward females, while the second sampling period showed a year with less trophic resources.

We highlight the results regarding the development time of *A. subaurarius*, which could be divided into two parts: a short development of about 30 to 60 days; and a delayed development, which can take more than a year. Another study carried out with another *Auplopus* species, found similar results, with a delayed development time that can take about 299.4 days (Buschini et al., 2007). This characteristic may be related to a long-term offspring investment, which can guarantee the adults' existence even after a period with less resources, such as winter. Seger (1983) proposed a model that explains the sex allocation to wasps and bees with overlapping generations and are bivoltine species, where the sex ratio should be male biased in the first overwinter generation and female-biased in summer generations. Despite that, this model does not consider multivoltine species (Buschini, 2007), and thus cannot fit the data of the present study. Therefore, future studies focusing only on this should be carried out to answer this question.

Knowing the strict relationship between parasitoid hosts and especially the availability of hosts that directly influences parasitoid maintenance (Tylianakis et al., 2006), we emphasize the importance of *A. subaurarius* conservation as this species acts as a regulator of the population of other arthropods and also regulates the maintenance of natural enemies, which also participate in other ecosystem processes. In our study, we found seven species of natural enemies of *A. subaurarius*, which were all other Hymenoptera species: *Ceyxia longispina*, *Caenochrysis crotonis*, *Photochryptus* sp.1, *Photochryptus* sp.2, *Messatoporus* sp., *Ephuta icema*, *Sphaeropthalma* sp. These natural enemies have many traits that were molded over time, which helps them to maximize the success of parasitizing their hosts, such as *A. subaurarius*. *Ceyxia longispina*, a Chalcididae species, was described by Andrade and Tavares (2009), and until now no study had reported its hosts. The genera *Ceyxia* has been associated with species that build their nests with clay, in addition to *Auplopus* species, parasitizing nests of *Trypoxylon* and *Sceliphron* (Andrade and Tavares, 2009). Unfortunately, we collected only two individuals of *C. longispina*, and there are no studies on their nesting biology traits, therefore we encourage future studies that aim to better describe how this species relates to its hosts inside their nests. On the other hand, *Caenochrysis crotonis* has been documented for its nesting habitats, also parasitizing other Pompilidae species, such as *Auplopus cf. brasiliensis* (Marinho et al., 2019). This species belongs to the Chrysididae family and it can be considered a kleptoparasite as their larvae feed on food stored by their hosts (spiders, in general) (Marinho et al., 2019).

Regarding natural enemies belonging to the Ichneumonidae family, which includes the genera *Photocryptus* sp. and *Messatoporus* sp., they have a long ovipositor which can be used to go deeper into the nests of their hosts (Vilhelmsen, 2003). A possible response of *A. subaurarius* to this natural enemy adaptation may be the dry plant material at the nest entrance and the closure plug in nests with larger cavity diameters (1 and 1.3 cm). A future study, aiming to answer this question may be important to better understand host-parasitoid relationships, and the adaptations between two co-evolving species. Another example of natural enemies that needs more studies are from Mutillidae family, in which little is known about their hosts, mainly in Neotropical regions (Aranda and Graciolli, 2016). We recorded two species of this family: *Ephuta icema* and *Sphaeropthalma* sp. For *Ephuta icema*, the first host record was made between 2015 and 2016 in the same area of our first sampling period (2017/2018), which was also *A. subaurarius* (Cambra et al., 2017). *Ephuta icema* seems to be an obligatory kleptoparasitoid as all the data until now on its genera suggest this (Cambra et al., 2017). Similarly, little is known about the interaction between *A. subaurarius* and the species of the genus *Sphaeropthalma* sp., despite having already been reported by Matthews (1997), in which *Sphaeropthalma pensylvanica* is the natural enemy species found. Therefore, there is still a great deal of work to be done on these species and basic studies on the nesting biology of wasp species, such as the one presented here, may be the beginning for future studies that aim to understand the interactions and evolution of species.

In conclusion, our study shows that the solitary wasp *A. subaurarius* could be found in different environments in the Atlantic Forest, such as *Araucaria* Forest fragments, grassland areas and *Eucalyptus* plantations. Moreover, we also saw that despite this apparent niche generality, regarding the habitat use, wooded environments may be important to *A. subaurarius* and their host maintenance. As observed, there was a higher abundance of *A. subaurarius* in the forest areas and *Eucalyptus* areas than in grassland areas and the reason for that may be the higher availability of resources, such as nidification sites, protection against predators and amount of food and hosts. Therefore, we emphasize the importance of wooded environments as many species of animals, such as *A. subaurarius*, may also have a greater dependence on these environments, although they are also found in other sites. By conserving native forest fragments and ensuring good silviculture plantation planning, considering ecological aspects of landscapes, we can maintain not only the presence of species, but also their interactions, and the ecosystem services provided by them.

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Supplementary Material

Supplementary material accompanies this paper.

Figure S1. Nests built by A. subaurarius in Guarapuava municipality, Paraná State, Brazil.
Figure S2. Nests built by A. subaurarius in Guarapuava municipality, Paraná State, Brazil.
Figure S3. Female and male of A. subaurarius collected in Guarapuava municipally, Paraná State, Brazil.
Table S1. Abundance difference of A. subaurarius between environments in two sampling periods (2017/2018 and 2020/2021). Bold values are significant.
Table S2. Auplopus subaurarius brood cell differences. Bold values are significant.

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