

Research Article

Use of Plant Resources by *Merosargus* (Diptera, Stratiomyidae, Sarginae) Larvae

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Received 7 August 2012; Revised 26 September 2012; Accepted 26 September 2012

Academic Editor: Kleber Del-Claro

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The genus *Merosargus* (Loew) has 142 described species. This great diversity in the genus could be explained by larvae resource-use specialization. However, information on larval habitats is still very scarce. In *Merosargus* species, adult males defend oviposition sites, and this territorial behavior may lead to interspecific competition and make even more important the specialization and niche partitioning to prevent competitive exclusion. This study identified substrate types used as a resource by *Merosargus* larvae and investigated the degree of specialization and overlap in resource use by different species at an Atlantic forest remnant in Minas Gerais, Brazil. Every potential resource, especially those with adults in the vicinity, was collected opportunistically from October 2001 to October 2004. In total, 292 individuals from 12 *Merosargus* species collected from 21 resource types and 15 plant species were reared in the laboratory. Plant species included herbs, vines, palms, and trees. Six *Merosargus* species were reared from only one resource type, and each resource type was used, on average, by less than two *Merosargus* species. Thus, *Merosargus* species exhibited a high degree of specialization and small overlap in larval resource selection, which could explain the high local and global diversity of the genus.

1. Introduction

The family Stratiomyidae (soldier flies) occurs in all warm temperate and tropical regions, especially in the wet tropics [1], and includes species with great morphological and habitat use diversity [2].

Little is known about Stratiomyidae larval biology in the Neotropical region. The larval stages of soldier flies have been extensively studied over the last decade in Brazil, but the studies focused mainly on larval and pupal morphology [3–12].

The genus *Merosargus* (Loew) is one of the largest in number of species in the family Stratiomyidae. Woodley [2] listed 142 species in the genus, and only two are not Neotropical. The previous revision of the genus is over 40 years old and listed only 109 species [13], thus the genus needs to be reviewed.

The biology of the genus is still poorly known. Woodley [2] reported the occurrence of *Merosargus* adults around various types of fruits and other rotting plant material on the forest floor, where males defend small territories, females oviposit, and mating occurs. He hypothesized that some species specialize on certain plant resources. Therefore, resource-use specialization by larvae could be an explanation for the great diversity in the genus. However, information on larval habitats is still very scarce and not species-specific [14–18].

In the Neotropical region, a wide variety of resources is available for phytophagous insects. Adult insects must recognize and select the best available oviposition substrates, and, for many species, resource quality has a major effect on their distribution and abundance [19]. The choice of oviposition sites is crucial for larval development and adult survivorship and vigor. In fact, several factors such as

nutritional quality, predation risk, and competition may act directly or indirectly in oviposition site selection [20].

Specialization in resource use is a way to maintain the coexistence of a large number of closely related insect species in tropical forests. However, recent studies have shown that different insect herbivore guilds exhibit different degrees of specialization and that some guilds such as chewers are predominantly generalists [21]. In addition, scavengers such as litter arthropods are often assumed to be generalists because they harvest nutrients from dead plant material and litter-decomposing microbes rather than directly interacting with living plants [22].

Conversely, specialization could be more important in cases where territorial defense occurs. Oviposition site defense is typical of species that use ephemeral resources and where females mate multiple times [23]. In these cases, last male sperm precedence is a common pattern [23, 24], and this behavior has been demonstrated in one *Merosargus* species [25]. Therefore, the defense of oviposition sites in *Merosargus* is very important to ensure mating just before oviposition. In fact, this behavior has already been observed in ten of the 18 *Merosargus* species found in our study site. Resident males avidly guard their territories repelling all intruders, including males of their own species or males and females of other species (Fontenelle et al. unpublished data). Therefore, strong interference competition could occur among *Merosargus* species using the same oviposition sites, which could lead to the exclusion of less combative species in the absence of resource use differentiation.

The understanding of oviposition site selection in *Merosargus* could not only explain the maintenance of high species diversity in the genus but also its origin, because assortative mating may occur in cases where males and females are attracted to a particular resource, which may have a prominent role in ecologically-driven sympatric speciation [26].

Thus, this study aimed to (i) identify the plant substrates used as a resource by *Merosargus* larvae, (ii) determine the period of the year when these substrates are used, (iii) investigate whether there are differences in the degree of specialization in resource use by different species, (iv) investigate whether there is an overlap in resource use by different species, and (v) determine which species use these resources similarly. Assuming that territorial defense leads to strong interspecific interference competition, we expect to find a high degree of specialization and low similarity in oviposition site selection among sympatric *Merosargus* species.

2. Methods

2.1. *Merosargus* Sampling and Rearing. Parque Estadual do Rio Doce (hereafter PERD), located between 19°48'18"–19°29'24" S, 42°38'30"–42°28'18" W, is an important Atlantic forest remnant in southeastern Brazil [27]. The PERD has an area of approximately 36,000 ha with a complex pattern of vegetation types [28]. The climate is humid, tropical, and mesothermal, with the rainy season from

October to March and dry season from April to September [29].

At least six Sarginae genera (*Merosargus*, *Ptecticus*, *Sargus*, *Microchrysa* Loew, *Acrochaeta* Wiedemann, and *Himantigera* James) and 18 *Merosargus* species have already been recorded in the PERD (Fontenelle et al. unpublished data).

This study was conducted opportunistically from October 2001 to October 2004. Sampling was done simultaneously to field campaigns from other studies that used malaise traps and that investigated the territorial behavior of *Merosargus* species associated to *Heliconia* conducted during this period. Therefore, the sampling effort was not the same for all periods of the year or all visited areas.

Samples were collected at six sites composed of semideciduous forests at different regeneration levels. We also sampled substrates in a forest fragment near the PERD with the same vegetation type, but an impoverished vertebrate fauna.

Every substrate that could theoretically be used by Sarginae larvae was collected. The sighting of adults on substrates or around their vicinity was considered the strongest evidence of larval occurrence. After first spotting adults on a particular substrate type that substrate was collected at subsequent field trips, even in the absence of adults, to better determine the larval occurrence period. A sample was considered a particular substrate type (plant structure) collected in the same place at the same date, often corresponding to a large amount of substrates.

The substrates were taken to the laboratory and kept in sealed chambers at room temperature until adults emerged. This paper only reports on collected substrates containing Sarginae larvae that resulted in the emergence of adults. Adult Sarginae were identified to genus level using the Woodley [30] identification key. *Merosargus* adults were identified to species level using James and McFadden's [13] key. Several species reared in our study could not be identified with certainty because taxonomic revision is needed for the genus *Merosargus*. Therefore, we chose to use the species names that are still uncertain only as a reference for possible species or the closest species; these species were, respectively, indicated in the result tables with "cf." or "aff." before the specific epithet. Voucher specimens were deposited in the Laboratório de Pesquisas Ambientais CODAAMB/IFMG-OP.

2.2. Data Analysis. Plant species and resource type specificity were determined using a host specificity index (H) [31]. This index is an estimate of the proportion of hosts used by a particular *Merosargus* species among all hosts available minus one

$$H = \frac{(S_F - 1)}{(S_T - 1)}, \quad (1)$$

where S_F is the number of plant species (or resource types) used by a *Merosargus* species, and S_T is the total number of plant species available. However, we modified the index replacing S_T by S_U , the total number of plants used by any *Merosargus* species. This was done because it was impossible to determine the actual availability of plant species as food

TABLE 1: Plant species and structure used as a resource by *Merosargus* larvae, month of occurrence, and number of *Merosargus* species found in samples collected at the Parque Estadual do Rio Doce (PERD), Minas Gerais, Brazil, between October 2001 and October 2004.

Plant species	(Structure)	Month of occurrence												Number of <i>Merosargus</i> species
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
<i>Panicum maximum</i>	(Pseudostem)	×												1
<i>Heliconia spathocircinata</i>	(Inflorescence)	×												2
	(Pseudostem)		×					×						2
<i>H. episcopalis</i>	(Inflorescence)	×		×	×									2
	(Pseudostem)				×			×	×		×	×		5
	(Bored pseudostem)								×					2
<i>H. amygdiana</i>	(Pseudostem)		×											1
<i>Thoracocarpus bisectus</i>	(Stem)		×					×				×		4
<i>Amaranthaceae</i> sp.2	(Leaf)			×										1
<i>Heliconia x matenensis</i>	(Inflorescence)			×										1
	(Pseudostem)			×								×		1
<i>Urera</i> sp.	(Stem)				×									2
<i>Cucurbitaceae</i> sp.1	(Leaf)				×							×		1
<i>Amaranthaceae</i> sp.1	(Leaf)					×								2
<i>Guarea</i> sp.	(Fruit)					×			×		×			1
<i>Astrocaryum aculeatissimum</i>	(Leaf)						×		×				×	3
<i>Euterpe edulis</i>	(Stem)								×					2
	(Inflorescence)								×					1
<i>Musa</i> sp.	(Pseudostem)								×					2
									×					1
<i>Lecythis lurida</i>	(Flower)												×	1
Number of resources/months		3	4	4	4	2	1	3	8	0	3	4	2	$S_{avg} = 1.81$
* <i>Joannesia princeps</i>	(Fruit)		×		×									0
* <i>Spondias</i> sp.	(Fruit)				×									0
*Unidentified	(Fruit)				×									0

S_{avg} : average number of *Merosargus* species found per resource type; *Plant resources used only by other Sarginae genera.

for *Merosargus* in the study area. However, this modified index underestimates specificity values compared to the original one.

We also used a measure of host specificity, calculated as

$$MH = 1 - H, \quad (2)$$

because higher specificity values should be attributed to more specialist species. Conversely, MH represents the proportion of hosts not used by a particular species, among all hosts available minus one.

The overlap in resource use was calculated using the Jaccard similarity index (J). We then constructed a cluster using the Jaccard distance ($1 - J$) as a measure of distance and the UPGMA amalgamation rule [32].

The Pearson correlation test was used [32] to test if the number of resource types used by each species was correlated with (1) the months when larvae were found, (2) the number of resources shared with other species, and (3) the average

Jaccard similarity index (J_{avg}) calculated by averaging the similarity in resource use of each *Merosargus* species with all remaining species.

3. Results

A total of 45 samples with *Merosargus* larvae were collected from 15 plant species, including herbs, vines, palms, and trees and 21 resource types including stems and pseudostems, leaves, fruits, flowers, and inflorescences (Table 1).

Most resources with larvae were collected during a few months ($M_{avg} = 1.76$ months) of the year. The resource most often sampled with larvae was *H. episcopalis* pseudostems (5 months). In addition, inflorescences of the same plant species were collected in three months. *Thoracocarpus bisectus* (Vell) stems were also sampled in three months. Several plant species containing larvae were collected in only one month. August was the month of the highest resource richness

TABLE 2: *Merosargus* species with respective plant species and substrate types found in samples collected at the Parque Estadual do Rio Doce (PERD), Minas Gerais, Brazil, between October 2001 and October 2004.

Merosargus species	Substrates	
	Substrate type	Plant species
<i>M. cf. arcuatus</i>	Stem	<i>T. bissectus</i>
	Stem	<i>T. bissectus</i> , <i>Urera</i> sp., <i>E. edulis</i> , and Cucurbitaceae sp.1
<i>M. azureus</i>	Pseudostem	<i>H. aemygdiana</i> , <i>H. x matenensis</i> , <i>H. spathocircinata</i> , <i>H. episcopalis</i> , and <i>P. maximum</i>
	Leaf	Amaranthaceae sp.2
<i>M. cf. bivittatus</i>	Inflorescence	<i>H. spathocircinata</i>
	Stem	<i>A. aculeatissimum</i> and <i>T. bissectus</i>
<i>M. cingulatus</i>	Pseudostem	<i>H. episcopalis</i>
	Leaf	<i>A. aculeatissimum</i>
	Inflorescence	<i>Musa</i> sp.
<i>M. cf. coxalis</i>	Flower	<i>L. lurida</i>
<i>M. gowdeyi</i>	Pseudostem	<i>H. episcopalis</i>
	Leaf	Amaranthaceae sp.1
	Stem	<i>A. aculeatissimum</i> and <i>Urera</i> sp.
<i>M. gracilis</i>	Pseudostem	<i>H. episcopalis</i>
	Leaf	<i>A. aculeatissimum</i>
<i>M. cf. opaliger</i>	Stem	<i>T. bissectus</i>
	Inflorescence	<i>Musa</i> sp., <i>H. episcopalis</i> , and <i>H. x matenensis</i>
<i>M. aff. pallifrons</i>	Pseudostem	<i>Musa</i> sp., <i>H. spathocircinata</i> , and <i>H. episcopalis</i>
	Bored pseudostem	<i>H. episcopalis</i>
<i>M. cf. pictipes</i>	Leaf	<i>A. aculeatissimum</i>
<i>M. cf. transversus</i>	Fruit	<i>Guarea</i> sp.
	Inflorescence	<i>H. spathocircinata</i> and <i>H. episcopalis</i>
<i>M. varicrus</i>	Pseudostem	<i>H. episcopalis</i>
	Bored pseudostem	<i>H. episcopalis</i>
Other Sarginae genera found		
<i>Acrochaeta</i> sp.	Stem	<i>T. bissectus</i>
<i>Ptecticus</i> sp.	Fruit	<i>Spondias</i> sp. and <i>J. princeps</i>
<i>Himantigera</i> sp.	Fruit	<i>Guarea</i> sp. and unidentified

sampled with *Merosargus* larvae ($N = 8$), while only in September plant resources with larvae were not sampled (Table 1).

Individual plant species hosted between 0 and 5 *Merosargus* species. A large proportion of plant species or resource types were used by only one *Merosargus* species. On average, only 1.81 *Merosargus* species were found per resource type (Table 1). The resources that were used by the largest number of species were *H. episcopalis* pseudostems ($N = 5$) and *T. bissectus* stems ($N = 4$). In addition, we never found more than two *Merosargus* species in any sample.

Most *Merosargus* species developed in vegetative organs such as stems, pseudostems, and leaves. However, *M. bivittatus* James, *M. coxalis* Lindner, and *M. transversus* McFadden used only reproductive organs (inflorescences, flowers, and fruits). Three species, *M. cingulatus*, *M. varicrus*, and *M. aff. pallifrons*, used both vegetative and reproductive organs, the latter represented by *Musa* sp. or *Heliconia* inflorescences.

Larvae of two other genera, *Ptecticus* sp. and *Himantigera* sp., also developed solely in reproductive organs of plants. The species *M. aff. pallifrons* and *M. varicrus* were also found in *H. episcopalis* pseudostems attacked by a lepidopteran borer (Table 2).

The plant samples resulted in the emergence of 361 Sarginae adults representing 15 species, including 292 individuals from 12 *Merosargus* species. The species with the highest number of adults were *M. azureus* (Enderlein) ($N = 121$) and *M. aff. pallifrons* (Curran) ($N = 58$) (Table 3).

The highest number of *Merosargus* species found in one month was five, in April and August (Table 3). In general, larvae of *Merosargus* species were collected during few months ($M_{\text{avg}} = 2.8$). The species found for the highest number of months were *M. azureus* ($N = 7$), *M. aff. pallifrons* ($N = 5$), and *M. varicrus* (James) ($N = 5$).

In total, six *Merosargus* species were reared from only one resource type. On average, few plant species ($S_{\text{avg}} = 2.5$) and

TABLE 3: *Merosargus* species, month of occurrence, number of adults reared in the laboratory, number of plant species and resources types (in brackets), and resource specificity of each species found in samples collected at the Parque Estadual do Rio Doce (PERD), Minas Gerais, Brazil, between October 2001 and October 2004.

Species	Month												Adults	Number of plant species (resource types)	Measure of specificity
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec			
<i>M. azureus</i>	×	×	×	×			×	×			×		121	10 (10)	0.36
<i>M. cf. bivittatus</i>	×												2	1 (1)	1.00
<i>M. aff. pallifrons</i>	×	×	×	×				×					58	4 (7)	0.79
<i>M. varicrus</i>	×			×				×		×	×		18	2 (4)	0.93
<i>M. cingulatus</i>		×		×				×				×	15	4 (5)	0.79
<i>M. gracilis</i>				×				×					9	2 (3)	0.93
<i>M. gowdeyi</i>					×					×			4	2 (2)	0.93
<i>M. cf. pictipes</i>						×						×	6	1 (1)	1.00
<i>M. cf. arcuatus</i>							×				×		36	1 (1)	1.00
<i>M. cf. opaliger</i>							×						4	1 (1)	1.00
<i>M. cf. transversus</i>										×			3	1 (1)	1.00
<i>M. cf. coxalis</i>												×	16	1 (1)	1.00
Species/month	4	3	2	5	1	1	3	5	0	3	3	3	Total = 292	$P_{\text{avg}} = 2.5$	$MH_{\text{avg}} = 0.89$
<i>Ptecticus</i> sp.		×		×									7	2 (2)	—
<i>Himantigera</i> sp.				×	×			×		×			50	2 (2)	—
<i>Acrochaeta</i> sp.							×						10	1 (1)	—

P_{avg} : average number of plant species found; MH_{avg} : measure of specificity (proportion of other plants species not used).

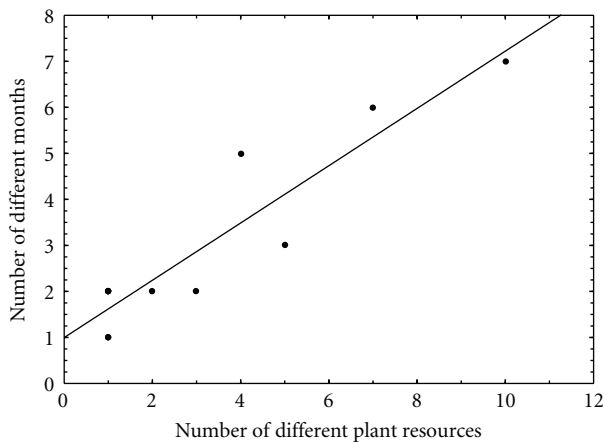


FIGURE 1: Relationship between the number of plant resource types used by *Merosargus* species and the number of months when larvae were found in samples collected at the Parque Estadual do Rio Doce (PERD), Minas Gerais, Brazil, between October 2001 and October 2004.

resource types ($R_{\text{avg}} = 3.1$) were used by each *Merosargus* species. The species that used the greater number of resources were *M. azureus* ($N = 10$), *M. aff. pallifrons* ($N = 7$), and *M. cingulatus* Schiner ($N = 5$). In general, species that used more plant resources were also found over a greater number of months ($r = 0.93$; Figure 1).

The average plant species host-specificity measure was $MH_{\text{avg}} = 0.89$ ($H_{\text{avg}} = 0.11$). This means that a *Merosargus*

species feeding on a particular plant species used an average of only 11% of other plant species used minus one.

Although over half of the plant species and resource types were used by a single *Merosargus* species, almost all species shared at least one plant species or resource type with another congener (Figure 2). The exceptions were *M. coxalis* and *M. transversus*, which used a single, exclusive resource type. *Merosargus azureus* used the largest number of exclusive plant species ($N = 5$) and resources types ($N = 6$).

As expected, generalist species were also the ones that shared the most resources with congeners ($r = 0.83$, $P < 0.05$; Figure 3). However, it should be noted that *M. cingulatus* exhibited greater resource overlap than expected from this correlation.

The small values of the Jaccard similarity index reflected the few overlaps in resource use between *Merosargus* species. The average similarity between a species and the remaining ones was below 25% for all species and below 15% for most species. There was no significant correlation between the number of resource types used and the average similarity indices (Figure 4). Most species exhibited similarity values between 10% and 15%, and this result was observed in more specialized species such as *M. arcuatus* James and *M. opaliger* Lindner as in relatively more generalist species such as *M. aff. pallifrons* and *M. azureus*.

The cluster analysis also reflected the small overlap in resource use by *Merosargus* species (Figure 5). The exception was the similarity between *M. arcuatus* and *M. opaliger*: as both used the same single resource their distance was zero in the cluster. Other than these species, *M. pictipes*, *M. gracilis*,

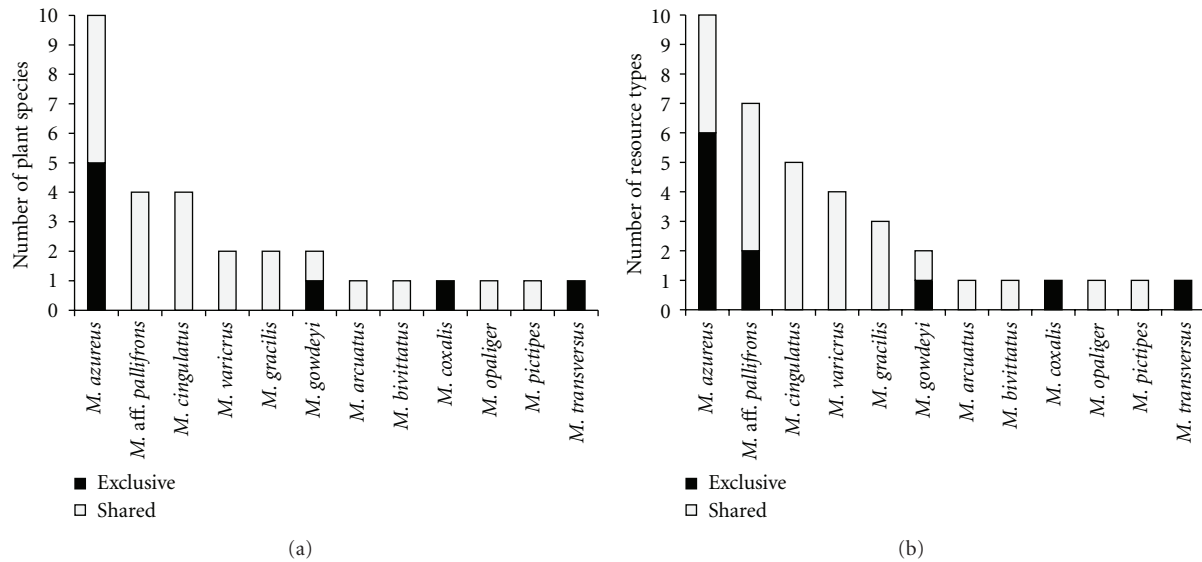


FIGURE 2: Number of plant species (a) and resource types (b) used by each *Merosargus* species found in samples collected at the Parque Estadual do Rio Doce (PERD), Minas Gerais, Brazil, between October 2001 and October 2004. Black bars represent plant species/resource types used by a single species, and open bars those shared with at least one species.

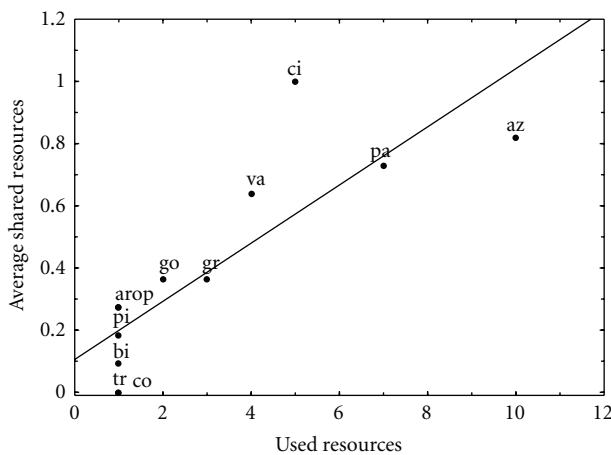


FIGURE 3: Relationship between the total number of plant resources used by *Merosargus* species and the average number of shared resources found in samples collected at the Parque Estadual do Rio Doce (PERD), Minas Gerais, Brazil, between October 2001 and October 2004. ar-*M. arcuatus*; az-*M. azureus*; bi-*M. bivittatus*; ci-*M. cingulatus*; co-*M. coxalis*; go-*M. gowdeyi*; gr-*M. gracilis*; op-*M. opaliger*; pa-*M. pallifrons*; pi-*M. pictipes*; tr-*M. transversus*; va-*M. varicrus*.

and *M. cingulatus* clustered together, and so did *M. pallifrons* and *M. varicrus*. In addition, the two species that used only different, exclusive resources, *M. transversus* and *M. coxalis*, were completely isolated from each other and from all the other species in the cluster.

4. Discussion

In our study we identified several plant species and structures where larvae of a significant number of *Merosargus* species

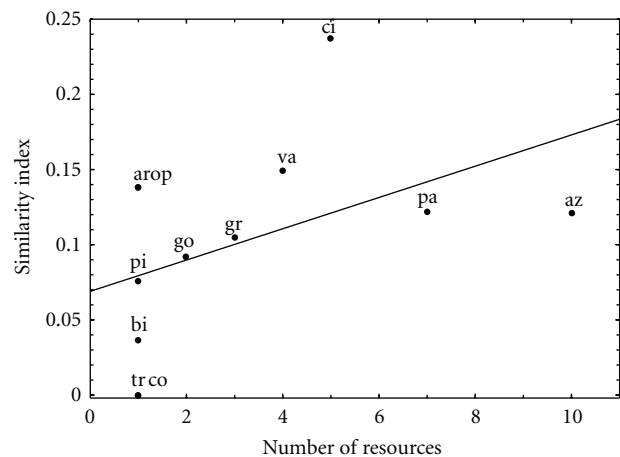


FIGURE 4: Relationship between the total number of plant resources used by each *Merosargus* species and the average Jaccard similarity index for each species from samples collected at the Parque Estadual do Rio Doce (PERD), Minas Gerais, Brazil, between October 2001 and October 2004. ar-*M. arcuatus*; az-*M. azureus*; bi-*M. bivittatus*; ci-*M. cingulatus*; co-*M. coxalis*; go-*M. gowdeyi*; gr-*M. gracilis*; op-*M. opaliger*; pa-*M. pallifrons*; pi-*M. pictipes*; tr-*M. transversus*; va-*M. varicrus*.

develop. We also showed that *Merosargus* uses a great diversity of substrates for larval development.

All plant species identified here, the genera *Panicum*, *Thoracocarpus*, *Astrocaryum*, *Euterpe*, *Guarea*, *Urera*, and *Musa*, and their respective families, except Arecaceae, shown here to be used by *Merosargus*, are new records. The plants of families Amaranthaceae and Cucurbitaceae whose genera were not identified are also new records for *Merosargus*. In fact, *Merosargus* larvae had only been previously observed

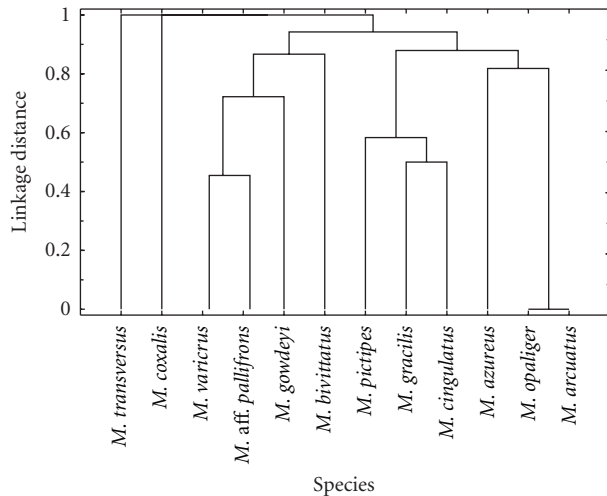


FIGURE 5: Cluster analysis of *Merosargus* species based on the similarity in resource use by the larvae from samples collected at the Parque Estadual do Rio Doce (PERD), Minas Gerais, Brazil, between October 2001 and October 2004. The cluster was constructed using the Jaccard distance $(1-J)$ and the UPGMA amalgamation rule.

in bracts of *Heliconia* (Heliconiaceae) inflorescences [14–16] and fallen flowers of *Couratari stellata* Smith (Lecythidaceae) [17]. Moreover, *Merosargus gracilis* had been recorded in another Arecaceae species (*Bactris gasipaes* Kunth) in the pulp of fruits [18], and not using the trunk or leaves as observed here for the two species of this family: *E. edulis* and *A. aculeatissimum*.

Oviposition occurs on substrates when they are recently damaged or already decaying. The predominance of herbaceous species as a resource for *Merosargus* could be explained by their soft tissues, which are more likely to be found damaged and more suitable for larval feeding. Damage to understory plants is especially likely to occur in the rainy season, when strong winds cause many trees to fall (Fontenelle pers. obs.). In addition, several animals can also cause plant damages. On several occasions, *M. azureus* males were observed approaching and establishing territories on damaged *H. episcopalpis* pseudostems immediately after agoutis had gnawed on them (Fontenelle pers. obs.). In fact, some gnawed pseudostems were sampled and yielded several adults of this species.

At the forest fragment in the vicinity of PERD, however, the vertebrate fauna is scarce and there may be less damage to the plants and less availability of vegetative resources for *Merosargus*. In contrast, may be less frugivory and a large amount of rotting fruit is found on the forest floor, which could be exploited by fly species that use fruit as resources.

Our data reinforced the strong association between *Merosargus* and *Heliconia*. There are five native *Heliconia* species at PERD: *H. episcopalpis*, *H. spathocircinata* (Aristeg.), *H. aemygdiana*, *H. angusta* (Vell.) [33], and *H. x matenensis* (Silva et al.) (*H. episcopalpis* and *H. spathocircinata* hybrid). Samples from only one native *Heliconia* species did not result in the emergence of *Merosargus* adults (data not shown).



FIGURE 6: Male of *Merosargus* cf. *varicrus* on the *Heliconia episcopalpis* pseudostem with rotten sheath.

There are also two exotic *Heliconia* species at PERD: *H. rostrata* (Ruiz & Pavón) and *H. psittacorum* (L.f.), but they were not sampled. Nevertheless, all *Heliconia* species found at PERD are likely used by *Merosargus* species.

Previous studies have shown *Merosargus* species using only the inflorescences of *Heliconia*. *Merosargus* larvae are part of the phytotelmata fauna of some *Heliconia* inflorescences whose bracts are filled with water and where larvae feed on rotten flowers and other debris [14–16].

Bracts of *Heliconia* species found at PERD do not accumulate large amounts of water. *Heliconia episcopalpis*, in particular, has small bracts that remain closed most of the time at an angle that prevents water accumulation, but the inflorescences have dozens of bracts where rotting flowers may be found (Fontenelle pers. obs.). Therefore, despite not collecting water, these inflorescences form an environment rich in rotten organic matter that is somewhat protected from predators and desiccation.

Pseudostems of the *Heliconia* species sampled are likely more important resources for *Merosargus* larvae than inflorescences. Pseudostems can be used in various forms and on several different occasions: when pseudostems of green plants are damaged or attacked by herbivores; when older leaves begin to rot; and when the entire pseudostem is in a more advanced state of decomposition. Bored pseudostems or with rotten sheaths have a strong bad smell. When the borer caterpillar chews on the central pseudostem shaft, it kills the inner leaf, which rots inside the pseudostem. Nevertheless, rotten sheaths are common in older plants and result from normal leaf senescence (Fontenelle pers. obs.).

Two *Merosargus* species, *M. aff. pallifrons* and *M. varicrus* (Figure 6), used both bored pseudostems and those with rotten sheaths (data not shown) and they were also found in inflorescences. In all instances larvae were found immersed in liquefied decaying organic matter subjected to heavy hypoxia.

In contrast *M. azureus* had a clear preference for fresh and newly damaged pseudostems (data not shown), which indicates that the volatile compounds that attract this species must be more associated to the plant itself than to its decomposition process.

Couturier et al. [18] found larvae of *Ptecticus* and *Merosargus* in Lecythidaceae flowers. They suggested that flower use is atypical in Stratiomyidae and occurs because of the fetid-scented flowers and the bat floral syndrome of the species of plants used by Stratiomyidae larvae. However, we found *Merosargus coxalis* using the flowers of *Lecythis lurida*, whose flowers are not particularly fetid and are bee-pollinated. Thus, we believe that flower morphology is more important than smell as an explanation for oviposition site selection by *Merosargus*. The morphology of Lecythidaceae flowers is quite distinctive, with stamens arranged in a ring protected by a hood-like, dense cluster of petals [34], forming a wet and safe environment for the larvae. Furthermore, the use of flowers by *Merosargus* larvae is not unusual, as they are very common in *Heliconia* flowers, and is not restricted to a specific floral syndrome, as the *Heliconia* species found at PERD are pollinated by hummingbirds [35].

In fact, several *Merosargus* species are attracted to the smell of rotten plant resources, although this is not true for all species identified in our study. We believe that different species are attracted to different volatile compounds, and the study of these compounds may help elucidate some of the mechanisms responsible for the resource preferences exhibited by different *Merosargus* species.

Additionally, resource preference can have a strong influence on the spatial distribution of populations. Other studies that sampled populations using more standardized methods showed that *Merosargus* species are concentrated in sites where large quantities of preferred resources are found. Sampling with malaise traps in areas with large *H. episcopalis* aggregations resulted in a large number of *M. azureus*, *M. varicrus*, *M. gowdeyi* (Curran), and *M. gracilis* (Williston) adults (Fontenelle et al. unpublished data), which further emphasizes the importance of this plant species as a resource for these insect species.

Because sampling was not uniform little can be said about the distribution of plant resources and species throughout the year. Few plant resources are found in only one season, but resource availability seems to increase during the rainy season.

Therefore, many resources are seasonally available, particularly plant reproductive organs, but vegetative parts may also be more available at certain times of the year. For example, trees fall mostly after the first rains, while borer caterpillars and agouti predation are more common in the dry season (Fontenelle et al. unpublished data).

Merosargus adults are also seasonal. However, more abundant species can be sampled throughout the year (Fontenelle et al. unpublished data), and their larvae and pupae are likely to be even more frequent than adults because the duration of these stages must be greater than that of the adult phase. Moreover, species that use less seasonal resources or a greater variety of resources available at different times could ensure the occurrence of larvae during several months of the year. Therefore, the relationship between the number of resources used and the number of months in which larvae were found should be interpreted with caution. In fact, this pattern may be explained by a correlation between both variables with the species abundance.

most abundant *Merosargus* species are likely to be found in more months and may have more known resources.

Merosargus species assemblages in individual plant species were species poor, as they only included up to five species. However, these figures are still higher than those observed for fruit flies (1–3) [31].

The average host specificity of fruit fly species relative to all plant species used as a resource found by Novotny et al. [31] was $H_{\text{avg}} = 0.02$. Using our modified index, the recalculated fruit fly H was $H_{\text{avg}} = 0.03$ for the genus *Bactrocera*, which used 25 plant species (1.67 plant species on average), and $H_{\text{avg}} = 0.13$ for the genus *Euphranta*, which used five plant species (1.50 plant species on average), a more similar result to the one found for *Merosargus* in our study.

We can assume that resource selection for larvae of the genus *Merosargus* is quite specialized. Moreover, we found few substrate types that were used by more than two species, leading to a slight overlap in resource use. Both specialization and little overlap in resource use may promote stable coexistence of *Merosargus* species. In fact, niche differentiation, and particularly resource partitioning, may promote the coexistence of closely related species (e.g., [36]).

Specialization in resource use is a possible explanation for the large number of closely related insect species found in tropical forests. However, some insect groups and guilds are predominantly generalists [21].

Most scavengers such as litter arthropods are often assumed to be generalists because they harvest nutrients from dead plant material and litter-decomposing microbes rather than directly interacting with living plants [22]. However, feeding niche differentiation was demonstrated and considered responsible for the high species richness and diversity of soldierless termites in neotropical rainforests [37].

When competition between members of different species occurs extreme conflicts are expected and the less successful competitor will either be driven to extinction or, more commonly, be forced to modify its feeding pattern [38]. Interspecific interactions among *Merosargus* adults include direct interference in resource use through territorial defense and monopolization (Fontenelle et al. unpublished data). Therefore, resource partitioning may be even more important in this genus as it is so diverse locally, even though males have such intense territorial behavior. Other mechanisms of resource partitioning may occur for species that were clustered together in the cluster analysis such as slight differences in adult activity time or area [38].

Genner et al. [39] studying territorial cichlid fish suggest that ecological generalism reduces the intensity of interspecific competition while specializations for the same resources increase it. We found that one of the most aggressive species *M. azureus* (Fontenelle et al. unpublished data) is the most generalist in resource use. Further studies on *Merosargus* territorial behavior, measuring the intensity of aggression intra- and interspecifically, and degree of resource monopolization will be essential to better understand the selective pressures leading to resource selection of this genus.

Considering the small sample size, the large number of single records, and especially the high plant diversity in forests of the study area, (over 1100 species) ([33, 40, 41]; see also [42] for a phytosociological study), we believe that only a small fraction of the potential resources available to *Merosargus* flies was sampled in this study.

Expanding the sampling effort to new plant species may reduce resource specialization estimates when additional resources are included. Conversely, it could also increase the estimates if additional *Merosargus* species with restricted resource ranges are included.

A taxonomic revision of the group, particularly using molecular techniques, may reveal host-specific cryptic species eventually masking the specialization as has occurred with other groups in Diptera [43, 44]. In addition, it remains to be studied if different genotypes, within a *Merosargus* species, prefer different resource types, an evidence of assortative mating that can act either increasing diversity, through sympatric speciation [26], as reducing the niche breadth [45].

Acknowledgments

The authors would like to thank the botanists Glauco Santos França, Julio Antonio Lombardi, João Renato Stehmann, and Tereza Cristina Souza Sposito for the identification of plant resources. They also thank José Roberto Pujol-Luz for sharing the invaluable literature and information on Sarginae identification. They are grateful to Flávia Barbosa and Bruno Madeira for reviewing the English version of the paper. The Instituto Estadual de Florestas (IEF) supported this work. This study is part of the long-term ecological program Pesquisas Ecológicas de Longa Duração (PELD) funded by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). CNPq also provided a Ph.D. scholarship to J.C.R. Fontenelle and a research grant to R.P. Martins.

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