Niche Overlap and Temporal Activity Patterns of Social Wasps (Hymenoptera: Vespidae) in a Brazilian Cashew Orchard

by

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ABSTRACT

The use of cashew fruits as a glucidic resource by wasps was quantified in an orchard to evaluate temporal overlap for a species-rich guild of social wasps and to determine if temporal partitioning within this guild reduces competition for food resources and facilitates species coexistence. Wasp activity was measured from 06:00 AM to 06:00 PM in a cashew orchard in Northeastern Brazil. A null model approach was used to evaluate temporal overlap for the entire guild of social wasps. Social wasp foraging time was bimodal and concentrated from 09:00 to 12:00 h and from 14:00 to 16:00 h. Overlap of temporal activity distributions between pairs of wasp species ranged from 0.58 to 0.83 (index of Schoener). Through analyses of temporal overlap for the entire guild, niche overlap among all species was greater than expected by chance. Social wasps show relatively high overlap in temporal activity patterns for all pairs of species (always over 50 percent) and in the analysis of the entire guild, average niche overlap among all pairs of species was greater than expected by the null model (n = 10,000 simulations). This indicated that interspecific interactions did not structure this wasp guild, and that responses to daily fluctuations in abiotic variables (*e.g.* temperature, humidity) likely structure activity patterns of these social wasps.

Key words – Community; Competition; Guild; Interactions; Polistinae.

INTRODUCTION

How predictable are characteristics of communities? Which aspects of community or guild structure are truly immutable properties? – Such

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questions are of broad interest to ecologists; moreover, determination of mechanisms that structure guilds and communities may have management and conservation implications. In general, research on guilds has focused on how coexisting populations of guilds are structured in space and on the influence of interspecific interactions (*e.g.* competition, facilitation) on such structure. More specifically, studies often evaluate how species partition habitats, food resources, and the abiotic environment to facilitate coexistence (Schoener 1986). Much less studied, but of equal importance, is the partitioning of the temporal niche dimension, which can reduce competition by decreasing the frequency of interspecific encounters of sympatric species that exploit a common resource base (Hölldobler & Wilson 1990, Kronfeld-Schor & Dayan 2003).

For species with similar ecological requirements to coexist, a partitioning of resources that allows multiple species to maintain sustainable populations must be achieved (Terborgh & Robinson 1986); such partitioning may be reflected by evolutionary trajectories of species (Walter 1991) but that is not always the case (Schoener 1986). However, division of resources by members of guilds and the resultant competitive structure can only be viewed as guild-level properties if they are maintained through time by competition for limiting resources (Pianka 1980). In this case, convergent use of abundant resources by non-competing populations or by populations under minimal competition (Connell 1980, Hairston 1984), which are included in the original concept of guilds (Root 1967), would not result in deterministic guild structure.

Time of activity and temporal activity patterns indicate how species exploit the environment and represent an important niche dimension (Pianka 1973). Species that occupy the same habitat and feed on the same resources may reduce competition by being active at different times, with such interactions leading to less temporal overlap than expected by chance. An other hand, if competition is not important to guild structure, temporal patterns of activity for ecologically similar species may be molded by shared responses to common external factors (*e.g.*, ambient temperature, predator avoidance), which may result in more temporal overlap than expected by chance (*e.g.*, Presley *et al.* 2009a, 2009b).

Recent studies on guilds of flower-visiting social wasps (Hermes & Köhler 2006, Aguiar & Santos 2007) and social wasps that collect glucidic resources from Cactacea fruit (Santos *et al.* 2007) show a high overlap in resource use. This leads to two hypotheses: (1) resources are sufficiently abundant such that coexistence of species in guilds of social wasps are not determined by resource partitioning; or (2) resources other than the Cactacea fruit itself are partitioned to permit coexistence. For example, species may partition time, with each species exhibiting a unique pattern of activity to reduce competition and permit coexistence. We evaluated temporal overlap for a species-rich guild of social wasps that use cashew fruits as a glucidic resource to evaluate if temporal partitioning within this guild reduces interspecific competition for food resources and facilitates species coexistence.

MATERIAL & METHODS

The study was conducted in the municipality of Biritinga, NE Brazil (11°37' S; 38° 49' W) in an 8-year old cashew orchard while trees had fully ripened fruits. The orchard comprised approximately 500 trees and covered 80,000 m^2. Samples were collected from 0600 to 1800 h for three consecutive days, during each of two harvest peaks: February 2003 and January 2004. Cashew fruits were simultaneously sampled by two collectors; the wasps were counted and fixed in 70 percent alcohol. Wasp samples were deposited in the insect collection of the Museu de Zoologia da UEFS (Zoology Museum, Feira de Santana State University). In our study the `fruit′ on which wasps forage is the peduncle that is comprised of a juicy pulp, which is botanically classified as a pseudo-fruit.

The numbers of wasp species and individuals foraging on cashew fruits during each time period were used to analyze the daily activity patterns and temporal niche overlap of cashew fruit use. To ensure even sampling throughout the orchard as well as to prevent a single plant or proximity to particular wasp nests from dominating estimates of temporal activity patterns, sampling time for each cashew plant was limited to 5 minutes.

The guild structure of social wasps that collect food from cashew fruits was characterized by using data on abundance of each species to calculate evenness and the Shannon (H') index of diversity. The overlap of trophic niches for each pair of wasp species was determined by the index of Schoener (1986), using $NO_{ih} = 1 - 1/2 \sum_k |p_{ik} - p_{hk}|$, where: "i" and "h" are the compared wasp species, p_{ik} and p_{hk} are ratios of individuals belonging to wasp species"i" and "h" collected during time period k, and p_{ik} is obtained by dividing the number of individuals in species "i" collected during k by the total number of individuals of species "i" collected during all sampling times. *Mischocyttarus* sp, *Polybia occidentalis* and *P. paulista* were not included in niche analyses due to low occurrence and low abundance in samples.

Kolmogorov–Smirnov 2-sample tests were used to evaluate interspecific differences in activity patterns between each pair of social wasp species (Siegel 1956). Contingency tables and chi-square tests were used to assess potential effects of presence/absence of each wasp species on presence/absence of other species within the same time period.

In addition, following Presley *et al.* (2009a), mean temporal overlap of the wasp assemblage was estimated via the Pianka (Pianka 1973) and Czechanowski (Feinsinger *et al.* 1981) indices. To compare our results with theoretical predictions, we assessed the significance of each overlap index (Pianka and Czechanowski) with a null model approach that uses a newly developed randomization algorithm, Rosario. In contrast with other null models, this algorithm maintains much of the temporal structure of activity patterns of each species, thereby restricting randomly generated patterns of activity to be biologically more realistic. In each iteration, Rosario shifts the entire activity pattern of each species a random number of time intervals and calculates the amount of overlap in the randomly generated set of activity patterns. Empirical values of overlap were compared to the respective null distributions of values generated via Rosario to determine significance with an α-level of 0.05. Software to perform analyses of temporal overlap is available at http://hydrodictyon.eeb.uconn.edu/people/willig/Research/activity%20pattern.html.

RESULTS

Ten species of social wasps were recorded in the cashew orchard (Table 1), with 7 species nesting in the orchard (N = 35 nests) and nine species observed foraging on cashew fruits (N = 304 individuals).

Polybia sericea was the most frequently found species foraging on cashew fruits, with 63 individuals and 20.72 percent of all observations. The next most frequently found species were *Polybia ignobilis* (*N* = 55, 18.09 percent), *Polistes canadensis* (*N* = 52, 17.11 percent), *Polistes versicolor* (*N*= 43, 14.14

Table1. Number of individuals and nests for each species of wasp as well as richness (S), diversity (H′), and evenness (J′) of social wasp individuals and nests in a cashew orchard during February 2003 and January 2004 in the municipality of Biritinga, Bahia, Brazil.

Species	Number of Individuals	Number of Nests	Nest Density (N/Ha)
Apoica pallens (Fabricius, 1805)	--	3	0.375
Brachygastra lecheguana (Latreille, 1824)	27	--	--
Mischocyttarus sp.	4	5	0.625
Polistes canadensis (Linnaeus, 1758)	52	12	1.500
Polistes versicolor (Olivier, 1791)	43	9	1.125
Polybia ignobilis (Haliday, 1836)	55	--	--
Polybia occidentalis (Olivier, 1791)	15	1	0.125
Polybia paulista Ihering, 1896	11	--	--
Polybia sericea (Olivier, 1791)	63	03	0.375
Protonectarina sylveirae (Saussure, 1854)	34	02	0.250
Total abundance	304	35	4.375
Wasp richness (S)	9	7	--
Wasp diversity (H′)	2.00	1.68	--
Wasp evenness (J′)	0.91	0.85	--

percent), *Protonectarina sylveirae* (*N*= 34, 11.18 percent), *Brachigastra lecheguana* (*N* = 27, 8.88 percent), *Polybia occidentalis* (*N* = 15, 4.93 percent), *Polybia paulista* (*N*= 11, 3.62 percent), and *Mischocyttarus* sp. (*N* = 4, 1.32 percent). Nest density of social wasps at the research site varied from 0.125 to 1.5 nests/ha; 3 species did not build any nests in the orchard.

Social wasp foraging time was bimodal (Fig. 1) and concentrated from 0900 to 1200 h (131 individuals, 43.1 percent of all observations) and from 1400 to 1600 h (85 individuals, 27.96 percent of the observations) (Kruskal-Wallis Test = 49.42, $P << 0.001$; F-Test = 9.99, $P << 0.001$). *Polybia sericea* (*N* = 31) and *Polistes canadensis* (*N* = 24) were most frequently found from 0800 to 1000 h, and *Polybia ignobilis* (*N* = 22) and *Polybia sericea* (*N*=17) from 1400 to 1800 h (Fig. 1).

Overlap of temporal activity distributions between pairs of wasp species ranged from 0.58 to 0.83 (index of Schoener) (Table 2), the highest being *Polybia sericea* and *Polistes canadensis* (index $NO_{ih} = 0.8300$), and *Polybia sericea* and *Polistes versicolor* (index $NO_{ih} = 0.8230$). Overlap of social wasp activity was relatively high for all pairs of species (always over 50 percent), with 11 of 15 pairs evincing > 70 percent overlap (Table 2). In analyses of temporal overlap for the entire guild, niche overlap among all species was greater than expected by chance (Pianka = 0.8594, $P < 0.0001$; Czechanowski = 0.8560, $P < 0.0001$).

Table 2.Temporal niche overlap (NOih Schoener index) between pairs of species of social wasps using cashew fruits (pseudo-fruit) as a food resource in the Biritinga area of Bahia, Brazil. Significance (P ≤ 0.05) of Kolmogorov–Smirnov 2-sample tests evaluating pair-wise differences in temporal activity patterns of social wasp species is indicated by an asterisk (*).

	Ba le	Po ca	Po ve	Po ig	Po se	Pr sy
Brachygastra lecheguana	-					
Polistes canadensis	0.7208	-				
Polistes versicolor	0.7700	0.8224	-			
Polybia ignobilis	0.6586	0.7332	0.7772	-		
Polybia sericea	0.8042	0.8300	0.82302	0.7628	-	
Protonectarina sylveirae	0.5839 *	0.8032 *	0.7018 *	0.6509 *	0.6909 *	-

DISCUSSION

Nine of the ten species of social wasp recorded in the cashew orchard foraged on cashew fruits. *Apoica pallens* nested in the area (three active colonies found in the orchard), but was not observed foraging on cashew; however, *A. pallens* has nocturnal and crepuscular habits (Nascimento & Tannure-Nascimento, 2005) and may have foraged in cashew during times that were not monitored in the study.

During most observations, at least three wasp species were found foraging simultaneously on the same fruit, with a maximum of 9 individuals representing 4 species foraging simultaneously.

Nest density of social wasps at the research site varied from 0.125 to 1.5 nests/ha; 3 species did not build any nest. The total density of 4.375 nests/ha is less than the density reported for Cerrado social wasps (D = 6 nests/ha) (Henriques *et al.* 1992) and greater than the density at the Caatinga de Ipirá (D = 3.23 nests/ha) (Santos *et al.* 2007).

Five of the possible15 pair-wise comparisons of activity patterns between social wasp species were significant (Kolmogorov–Smirnov test) (Table 2). All significant differences involved *Protonectarina sylveirae* suggesting that this species had relatively distinctive activity patterns compared to other syntopic wasps (Fig. 1). The chi-square tests confirm these results; each species of the Biritinga´s social wasp assemblage showed significantly negative associations with *Protonectarina sylveirae*. In contrast, the remaining species of wasp did not show any positive or negative patterns of co-occurrences with each other.

Social wasps show relatively high overlap in temporal activity patterns for all pairs of species (always over 50 percent) and in the analysis of the entire guild, average niche overlap among all pairs of species was greater than expected by the null model (n = 10,000 simulations). This indicated that interspecific interactions did not structure this wasp guild, and that responses to daily fluctuations in abiotic variables (*e.g.* temperature, humidity) likely structure activity patterns of these social wasps.

The large number of social wasp individuals and species using cashew fruits as a food resource shows the importance of cashews to social wasps during

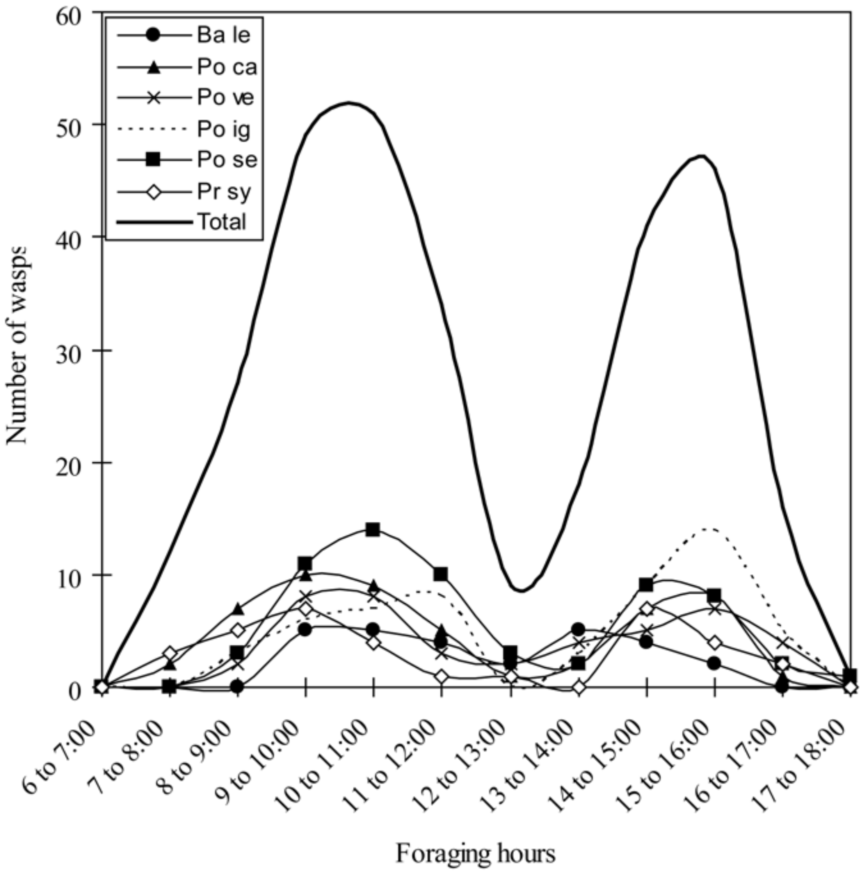

Fig. 1. Temporal activity patterns of foraging social wasps from 0:600 to 18:00 h on cashew fruit (pseudo-fruit) in Biritinga, Bahia, Brazil.

early parts of the year. The association of individuals of different species using an important food resource at the same location and time, and with no effect of one species on the presence or absence of others shows that the resource is available in greater amounts than required by all wasp populations in the guild. Moreover, wasps may focus on efficient harvest during times of abundant, ephemeral resources such as cashew fruits, which may temporarily alter the nature of interspecific interactions that may manifest when resources are less plentiful. Although many fruits were regularly visited simultaneously by different species, most fruits in the orchard were never visited and cashew fruit availability did not limit the presence or abundance of wasp species for this guild. The amount of available cashew fruits was many times greater than could be harvested by all of the social wasp populations visiting the orchard. Our results corroborate the conclusions drawn by Pianka (1980, 1994): that resource abundance can negate potential interspecific competition in a guild.

The social wasp guilds feeding on glucidic resources of cashew fruits in Biritinga have a nested pattern of occurrence and competition is weak or absent. These results support the theory that guilds can reveal the convergent use of abundant resources by non-competing populations. There is widespread evidence that different guilds can be structured as a function of competition (*e.g.*, Johnson 1986, Sousa 1993).

Several species of social wasps damage fruits in commercial orchards (*e.g.*, Hickel & Shuck 1995, Silva *et al.* 1968). Food scarcity is the primary reason that wasps attack grapes (Hickel & Shuck 1995, Silva *et al.* 1968), as intensive agricultural crop systems typically reduce local flora diversity to such low levels that naturally occurring insect populations can not be maintained throughout the year. Silva *et al.* (1968) reported that wasp attacks on grape orchards during times of fruit maturation coincided with periods of scarcity of natural floral resources. Wasps and bees prefer flower nectar to other sweet exudates (*e.g.*, fruit juices of honeydew; Hickel & Shuck 1995) and attack agricultural crops only out of necessity. In contrast to detrimental effects of wasps on other agricultural crops, wasps that feed on cashew did not perforate intact fruits (pseudo-fruits), despite the large number of social wasps foraging on cashew fruits throughout the day. Rather, wasps collected pulp by digging at natural cuts and pre-existing damage caused by Irapuás (*Trigona* sp.). Although they did not create newly damaged areas on the fruit, this activity did significantly worsen the health of the affected areas of the pseudo-fruits.

Wasps will not damage intact fruits but their presence on fruits or nests associated with the orchard can decrease harvest efficiency by intimidating farm workers. Nonetheless, wasps benefit orchards by reducing populations of pest-insects in crops. During our study, we observed social wasps preying on the white-fly (*Aleurodicus cocois*) on cashew leaves: *Polybia ignoblis* (3 observations*), Polybia sericea* (2 observations), *and Polistes canadensis* (1 observation). This pest negatively affects cashew crops by extracting large quantities of phloem sap, which can result in greater than 50 percent yield reduction. Additionally, the honeydew excreted by these insects serves as a medium for sooty mold fungi and can be the vectors of several important plant pathogens (Byrne & Bellows 1991). Consequently, social wasp likely represent a net positive influence on cashew crops.

In general, it is expected that species of the same guild should partition niche axes to facilitate coexistence and persistence of each species. In contrast, studies based on a mechanistic approach to the niche concept show that this expectation is dependent on the types of traits involved. If traits are related to species' requirements or to tolerance of abiotic environmental factors, locally coexisting species should be more similar in such traits than expected on the basis of random assortment (Leibold 1997). The basis for this expectation is that all species in a local guild must be adapted to the same environmental conditions and must be able to exploit more-or-less the same resources bases. If competition structured local guilds it is likely that competitive exclusion would have prevented local coexistence. That many similar species can coexist locally suggests that adaptation to environmental conditions are more important in structuring local guilds than are interspecific interactions. It is important stress that, up to now, most studies of guilds or assemblages do not show temporal niche segregation (Presley *et al.* 2009a, 2009b, Castro-Arellano *et al.* 2009), which may indicate that temporal activity patterns are an important characteristic of local guilds and that those effects over-ride potential effects of interspecific competition on use of time.

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