Fluctuations in Richness and Abundance of Social Wasps During the Dry and Wet Seasons in Three Phyto-Physiognomies at the Tropical Dry Forest of Brazil

G. M. DE M. SANTOS,1,2 P. C. BISPO,3 AND C.M.L. AGUIAR1


ABSTRACT The social wasp nests were quantified in three different plant physiognomies (forested Caatinga, shrubby Caatinga, and agricultural systems) to analyze the effect of environmental seasonality and plant physiognomy on the richness, nest abundance, and species composition of social wasps in the region of tropical dry forest of Brazil. The forested Caatinga physiognomy had the greatest richness of species ($S=16$), followed by shrubby Caatinga ($S=13$) and by agricultural system ($S=12$). The first axis of detrended correspondence analysis (DCA) explained 67.8% of the variability and shows a gradient of the fauna from agricultural system and shrubby Caatinga to forested Caatinga. In the first axis, wet season scores were much higher than those for the dry season in forested Caatinga. The second axis explained 18.7% of the variability and shows a separation of samples collected during the wet or the dry periods in shrubby Caatinga. This separation was less evident in the agricultural system. Variations in nest abundance were more intense in arbustive caatinga (45% decrease in number of active nests in the dry period), moderate in forested Caatinga (24% decrease in number of active nests in the dry period), and low in agricultural systems (8% decrease in the dry period).

KEY WORDS Caatinga, Polistinae, community ecology, species richness

Studies on diversity of social wasps (Hymenoptera: Vespidae) in Brazilian ecosystems are still scarce and several refer to the classic studies by Ihering (1904), Duche (1906, 1910), Richards and Richards (1951), and Richards (1978). Recent research have produced information on the biodiversity of social wasps in the cerrado (Henriques et al. 1992, Diniz and Kitayama 1998, Mechi 2005, Elpino-Campos et al. 2007, Santos et al. 2009), rupesrian fields (da Silva-Pereira and Santos 2006), caatinga (Santos et al. 2006, Aguiar and Santos 2007), the Atlantic Forest, mangroves and sandbanks (Santos et al. 2007), Araucaria Forest (Hermes and Köhler 2006), and in agriculture lands (Marques and Carvalho 1993, Hermes and Köhler 2006).

The diversity and seasonality of species in social wasp communities are usually studied from two perspectives: abundance of flower-visiting wasps (Santos et al. 1998, 2006; Silva-Pereira and Santos 2006; Hermes and Köhler 2006) or nest abundance (Henriques et al. 1992, Marques and Carvalho 1993, Diniz and Kitayama 1994, de Santos et al. 2007). This paper is based on nest abundance.

The temporal dynamics of tropical social wasps is very complex. These insects contribute significantly for their colonies and do not abandon them easily; the colonies can be considered semisessile organisms (Santos and Gobbi 1998). Studies on nest abundance have shown that seasonality occurs in some neotropical social wasps species but not in others (Marques et al. 1992, Ramos and Diniz 1993, Diniz and Kitayama 1998, Santos et al. 2006). Furthermore, the same species may present seasonal fluctuation or not, depending on environmental conditions (Ramos and Diniz 1993).

The semiarid region in the Brazilian Northeast has two well-defined seasons: the dry and the wet seasons. For our purposes, the definition of “dry period” involves scarce food resources for the entomofauna. Conversely, the “wet period,” which extends for 2 mo after the rain stops, presents intense plant blooming and abundance of food resources for the entomofauna.

This study aimed to investigate the relationships between richness and abundance of wasp species and plant physiognomies with different levels of complexity (agricultural systems, shrubby Caatinga, and forested Caatinga) in a tropical dry forest region of Brazil (Caatinga). It also aimed to understand whether the fluctuations in richness and abundance of wasp nests in these communities are related to the wet and dry seasons.

Materials and Methods

The study was conducted in the municipalities of Itatim (12°42’ S and 39°41’ W), Itaberaba (13°32’ S and 40°18’ W), and Milagres (12°52’ S and 39°51’ W), State
of Bahia, northeastern Brazil. This is a semiarid tropical region with high risk of drought. The landscape is a mosaic of agricultural environments and several physiognomies of the natural caatinga vegetation. Samples were collected at all three locations from each of the following physiognomies: FC, forested caatinga, seasonally dry tropical semideciduous forest, 6–16 m high; SC, shrubby Caatinga, open physiognomy with predominance of medium-sized vegetation (<2 m high), important presence of cactuses and palm trees; AS, agricultural systems, where the natural vegetation was partially replaced by pasture or small plots of crops (cowpea, *Vigna unguiculata*; beans, *Phaseolus vulgaris*; corn, *Zea mays*).

The number of nests with active colonies in each physiognomy was used as measure of abundance. Two data collectors searched for nests of social wasps with active colonies in each physiognomy, during the wet period (January, February, and July 1998) and the dry period (September, October, and November 1998). Each collector searched for 80 h in each physiognomy, a total of 160 h of sampling for each physiognomy. Five to 10 specimens from each colony were registered and identified. Individuals of all species were deposited in the Entomological Collection Johann Becker of the Museu de Zoologia of the Universidade Estadual de Feira de Santana (MZUEFS).

Because of the important variation in number of nests among plant physiognomies, we used rarefaction curves to compare the richness of species for the same number of nests. K individuals were randomly removed from the sample to estimate the taxa number. The procedure was repeated 1,000 times with the program Ecosim 5 (Gotelli and Entsminger 2000). The abundance matrix was logarithmized before the analysis. This matrix was submitted to detrended correspondence analysis (DCA) (Gauch 1995, Legendre and Legendre 1998) using the program PCORD (McCune and Mefford 1999). The Mantel test was used to evaluate the relationship between complexity of the habitat (Euclidian distance among the samples based on a scale of habitat complexity) and the fauna (Morisita-Horn similarity index). The scale of habitat complexity varied from 1 to 3. The value 1 was attributed to agricultural systems, 2 to shrubby Caatinga, and 3 to forested Caatinga. The Mantel test was done with 5,000 permutations in NTSYS 2.1 (Rohlf 2000).

### Results

Three hundred nineteen nests of 17 species of social wasps were observed. Some of these nests were active in both dry and wet seasons; thus, we had 489 nests registered (Table 1). The forested Caatinga physiognomy had the greatest richness of species ($S = 16$), followed by shrubby Caatinga ($S = 13$) and the agricultural system ($S = 12$) (Fig. 1). The most abundant species were *Polistes canadensis canadensis* (L., 1758), *Polybia sericea* (Olivier, 1791), *Polybia ignobilis* (Haliday 1836), *Polybia o. occidentalis* Richards, 1951, *Brachygastra lecheguana* (Latreille, 1824), and *Polistes versicolor versicolor* (Olivier, 1791); they

### Table 1. Number of social wasp nests registered in three Caatingas physiognomies during the wet and the dry seasons in Brazil

<table>
<thead>
<tr>
<th>Species</th>
<th>Agricultural system</th>
<th>Shrubby Caatinga</th>
<th>Forested Caatinga</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dry</td>
<td>Wet</td>
<td>Dry</td>
</tr>
<tr>
<td><strong>01</strong> A. pallens (Fabricius, 1804)</td>
<td>3</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td><strong>02</strong> Brachygastra lecheguana (Latreille, 1824)</td>
<td>16</td>
<td>16</td>
<td>8</td>
</tr>
<tr>
<td><strong>03</strong> Clypearia angustior Ducker, 1906</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><strong>04</strong> Mischocyttarus cassununga (Ihering, 1903)</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><strong>05</strong> Mischocyttarus cerberus Ducker, 1918</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><strong>06</strong> Mischocyttarus dresveni Saussure, 1857</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><strong>07</strong> Parachartergus pseudacalis Willink, 1959</td>
<td>1</td>
<td>2</td>
<td>—</td>
</tr>
<tr>
<td><strong>08</strong> Polistes b. bidentirii (Fabricius, 1804)</td>
<td>2</td>
<td>3</td>
<td>—</td>
</tr>
<tr>
<td><strong>09</strong> Polistes c. canadensis (L., 1758)</td>
<td>35</td>
<td>33</td>
<td>11</td>
</tr>
<tr>
<td><strong>10</strong> Polistes c. versicolor (Olivier, 1791)</td>
<td>7</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td><strong>11</strong> Polybia iguabilis (Haliday, 1836)</td>
<td>22</td>
<td>21</td>
<td>5</td>
</tr>
<tr>
<td><strong>12</strong> Polyphla o. occidentalis Richards, 1951</td>
<td>18</td>
<td>27</td>
<td>1</td>
</tr>
<tr>
<td><strong>13</strong> Polybia paulistana von Ihering, 1896</td>
<td>3</td>
<td>6</td>
<td>—</td>
</tr>
<tr>
<td><strong>14</strong> Polybia sericea (Olivier, 1791)</td>
<td>19</td>
<td>14</td>
<td>24</td>
</tr>
<tr>
<td><strong>15</strong> Protonectarina sylveirae (Saussure, 1854)</td>
<td>2</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td><strong>16</strong> Protopolyibia c. exigua (Saussure, 1854)</td>
<td>1</td>
<td>3</td>
<td>—</td>
</tr>
<tr>
<td><strong>17</strong> Synoeca cyanea (Fabricius, 1775)</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><strong>Total (N)</strong></td>
<td>129</td>
<td>140</td>
<td>55</td>
</tr>
</tbody>
</table>
corresponded to 82.4% of all colonies of social wasps (Table 1).

The number of active nests observed varied among physiognomies: 171 in the agricultural system, 105 in shrubby Caatinga, and 43 in forested Caatinga. After standardization by rarefaction (40 nests), the richness (Figs. 1 and 2) of agricultural system and shrubby Caatinga were similar but lower than in forested Caatinga.

Standardized richness for the same number of colonies in each plant physiognomy was similar between the wet and the dry periods for the agricultural system and for the forested Caatinga (Fig. 3). However, richness in shrubby Caatinga was much greater in the wet period.

A significant relationship between the complexity of plant physiognomies and the fauna of wasps was observed (Mantel test, \( r = -0.584; P = 0.0002; 5,000 \) permutations). Species and sample dispersion in a bi-dimensional space formed by the two first axes of the DCA are presented in Fig. 4. The first axis of the DCA explained 67.9% of variability and shows a species gradient from agricultural system and shrubby Caatinga to forested Caatinga. In the first axis, wet season scores were much higher than those for the dry season in forested Caatinga (Fig. 4). The second axis explained 18.7% of the variability and shows a separation of samples collected in the wet and the dry periods in the shrubby Caatinga. This separation was less evident in the agricultural system because of the overlap of samples collected in both seasons (Fig. 4).

The abundance of nests between the dry and the wet periods varied. Variations were more intense in shrubby Caatinga (45% decrease in number of active nests in the dry period), moderate in forested Caatinga (24% decrease in number of active nests in the dry period), and low in agricultural systems (8% decrease in the dry period).

Discussion

Community ecology theory states that complex environments with greater structural heterogeneity can keep a larger number of species. Greater environmental heterogeneity allows for a larger number of niches, setting the conditions for a larger number of species to coexist (Levins 1962, Stehli et al. 1969, Latham and Ricklefs 1993, Bragança et al. 1998). Data presented in this study only partially agree with the above. On the one hand, the greatest richness of social wasps was found in the physiognomy with the highest heterogeneity, the forested Caatinga. On the other, although agricultural systems are structurally simple and comparatively much more homogeneous than shrubby Caatinga, both physiognomies presented similar values for richness. Agricultural systems have relatively simple vegetation structures but high availability of food resources (nectar, preys, and water) for social wasps throughout the year. The same does not occur in shrubby Caatinga, where resource availability is highly seasonal.

Shrubby Caatinga, the physiognomy with the most susceptible fauna to seasonal changes, barely had water, green vegetation, flowers, or fruits in the peak of the dry period (November); food scarcity led to smaller numbers of species and nests registered compared with the wet period. In forested Caatinga and in agricultural systems, food resources for wasps were also available during the driest periods, probably because of flora diversity, varied phenological patterns in forested Caatinga (e.g., occurrence of species that bloom during the dry season or throughout the year), and water management in agricultural systems. As a result of greater stability in resource availability, the richness and nest abundance of social wasps registered in both physiognomies was less susceptible to local seasonal variations than shrubby Caatinga.

Rainfall, frequent during the wet period in the caatinga, affects the seasonal availability of floral resources and leads to a seasonal pattern of resource use by wasps (Diniz and Kitayama 1998, Santos et al. 2006, Aguiar and Santos 2007). Wasp foraging activity is intense during the wet season and significantly decreases during the dry season (Santos et al. 2006). Elpino-Campos et al. (2007) reported that, during the dry season in the Cerrado (another South American dry forest with a well-defined dry season) in central
Brazil, the decrease in water and food availability (nectar and preys) are limiting factors for colony survival. Lorenzon et al. (2003) observed that, in caatinga environments, social bees decreased foraging activities during the dry season. Considering that eusocial colonies of social wasps need a permanent food supply, food storage is the only guarantee for colony survival during scarcity periods.

The effects of plant physiognomy and season were important determinants of the wasp fauna because samples collected in the same physiognomy and same season were quite similar. Wasp faunas were different in each of the three phyto-physiognomies studied, showing the importance of the vegetation mosaic to maintain wasp beta diversity. Some wasp species increase abundance or occur only in the wet season, reinforcing the effect of seasonality on wasp fauna.

Our data showed that, in addition to factors intrinsic to each species, such as the ability to forage and store food, the dynamics of social wasps is strongly influenced by environmental factors such as local vegetation structure and the seasonal variations in food and water availability.

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Received 11 May 2009; accepted 13 August 2009.