Seasonal variation in black fly (Diptera: Simuliidae) taxocenoses from the Brazilian Savannah (Tocantins, Brazil)

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ABSTRACT: We investigated the spatial and temporal distribution of blackfly larvae on a mesohabitat scale at four different breeding sites in the Brazilian savannah “Cerrado.” A total of 2,385 larvae of 12 different species were collected, and three of the sampling sites revealed species richness and diversity peaks in April. A principal components analysis was performed to reduce abiotic data into a smaller set of independent variables, such as precipitation and river size, and subsequent linear regressions showed that Simulium subpallidum was positively correlated with precipitation. This species, along with S. nigrimanum, was negatively correlated with river size, whereas S. perflavum was negatively correlated with precipitation. Beta diversity was negatively correlated with precipitation, and black fly taxocenoses were markedly different between wet and dry seasons, as shown through nonmetric multidimensional scaling, suggesting that precipitation plays a major role in structuring these communities, probably because of enhanced drift and the dendritic nature of lotic metacommunities. Journal of Vector Ecology 39 (2): 321-327. 2014.

Keyword Index: Seasonal distribution, black flies, precipitation, beta diversity, Cerrado.

INTRODUCTION

Black fly larvae are often significant components of lotic ecosystems and are usually present at very high densities. They are important in such ecosystems as a prey resource to many macroinvertebrate and fish predators (Werner and Pont 2003) and because of their role as a trophic link (Kazanci and Ertunç 2010, Başören and Kazanci 2011).

Although black fly larvae are usually regarded as classic examples of filter-feeding organisms, results show that they capture suspended particles nonselectively from the water column (Hershey et al. 1996, Wotton 1996, Ciborowski et al. 1997). Scraping and collecting are other feeding techniques often observed in these organisms (Colbo and Wotton 1981).

Black fly larvae are usually present in almost every lotic habitat type, and they are often found at very high densities in lake and reservoir outlets (Sheldon and Oswood 1977; Wotton 1987; Malmqvist 1994). The pest potential of black flies is influenced by many factors, such as breeding site characteristics, seasonal abundance, flight range, mating, and oviposition behaviors (Lake and Burger 1983). The major breeding site characteristics associated with the distribution and population dynamics of black fly larvae are distance from lake or reservoir outlets, stream/river size, food supply, substratum, current velocity, depth, light, and physicochemical conditions (Ross and Merrit 1987, McCreadie et al. 2006, Rahba et al. 2013).

Only a few studies have investigated the distribution and population dynamics of Neotropical black flies larvae (Figueiró et al. 2006, 2008, Coppo and Lopes 2010, Santos et al. 2010), and most of those studies were concentrated in just a few biomes such as Amazonia and Mata Atlântica (Figueiró and Gil-Azevedo 2010). Biotic factors may strongly affect community structure in lotic systems, whereas abiotic factors are believed to play a dominant role in shaping species assemblages (Allan 1995). However, changes in species composition and community structure across stream sections reflect responses to environmental gradients and dispersal abilities (Heino 2009), whereas variations in species composition among local stream communities is a result of local abiotic and biotic conditions and large-scale factors such as dispersal (McCreadie and Adler 2012).

The aim of this study was to identify the main abiotic factors influencing the spatial and temporal distribution of black fly larvae assemblages and population dynamics of black fly larvae on a regional scale. This study, together with those of Landeiro et al. (2009) and Figueiró et al. (2012), is one of the first contributions to the knowledge of the ecological traits of neotropical black fly larvae of the “Cerrado.” The black fly fauna of this biome, which is the second largest area extension in Brazil, is still poorly known.
MATERIALS AND METHODS

The “Cerrado” biome comprises an area of approximately 204.7 million h, which corresponds to 24% of the country's territory (IBGE 2004). Approximately 30% of Brazil's biodiversity is contained within this biome (Dias 1996). The Tocantins state presents two well-defined seasons, a rainy season (October–March) and dry season (April–September).

Sampling was conducted at four selected sites. Three were small tributaries of larger rivers and one was a small section of the Tocantins River beside the construction of the Peixe Angical hydroelectric scheme (Figure 1).

Site A: Córrego do Mato (12° 39'33.0"S, 048° 18'27.3"W)

This site has been classified as a first-order tributary (Strahler 1952) of the Tocantins River. It presents a mean width of approximately 5 m and a mean depth of 1 m. It is characterized by a dense canopy cover that provides shade for the water course, and it has a predominantly rocky bed. It also features a small artificial reservoir.

Site B: Córrego Piabanha (12° 45'07.8"S, 48° 17'16.6"W)

This site has been classified as a second-order tributary of the Tocantins River (Strahler 1952) and has an average depth of 1 m and a mean width of 8 m. It is characterized by a rocky bottom and riparian vegetation formed by 50-cm to 1-m shrubs very close to the stream, which provide little shade for the margins and have partially submerged branches.

Site C: Ribeirão das Lages (12° 35'7.7"S, 48° 2'29.2"W)

This site has been classified as a first-order tributary of the Paranã River (Strahler 1952). It has an average depth of 1 m and a mean width of 10 m, therefore resulting in no canopy cover (vegetation occurs along the water course margin, but the canopy does not provide shade for the stream) and a sandy bottom.

Site D: Tocantins River (12° 13'05.5"S, 48° 25'56.7"W)

This site is a river that averages 4.5 m in depth and 600 m average width. It has very pronounced riparian vegetation with branches submerged in the water; however, the vegetation provides little shade due to the great width of the river.

Abiotic factors

pH and mean water current velocity measurements were taken at each site during each sampling. Streambed particle size and riparian vegetation were estimated according to McCreadie and Colbo (1991), and precipitation, humidity, and temperature were obtained for each sampling date from the data of the National Institute of Meteorology.

Larval sampling

Later instar black fly larvae were manually sampled from the four study sites during six bimonthly sampling periods from October, 2004 to August, 2005. At each sampling site, which consisted of a 15 m stream/river section, a random stratified sample of 15 quadrants (30 × 30 cm) was taken during each sampling.

Larval identification

The larvae of all instars were sorted into morphotypes according to their general morphological characteristics and their cephalic spots. Subsequently, last instar specimens from each morphotype were dissected, mounted on slides, and identified by direct comparison with pupae collected at the sites and material deposited at the Laboratório de Simulídeos e Oncocercose/Instituto Oswaldo Cruz, with the aid of a taxonomic bibliography (Coscarón and Coscarón-Arias 2007, Hamada and Adler 2001).

Principal components analysis (PCA) was performed using the presence/absence data matrix to evaluate the abiotic factors acting in the mesohabitat distribution of black fly taxocenoses. The principal components (PCs) were interpreted through Spearman's rank correlation analyses, relating the original variables with the newly formed PCs, and subsequent linear regressions were performed using the PCs as predictors and species as dependent variables, according to McCreadie et al. (2006) (Table 1). Nonmetric multidimensional scaling (NMDS) was performed with overall species abundances from each sampling date to evaluate seasonal variations in the taxocenoses. Beta diversity was calculated using the Whittaker beta diversity index (Whittaker 1960) for each pair of sites in each of the first five sampling dates, and the mean value of these indices was used for each date to evaluate the effect of rain on a regional level.

The sixth sampling date was excluded from the data analysis because three of the study sites were no longer suitable breeding sites for black fly larvae because of the influence of the nearly completely functional Peixe Angical hydroelectric scheme. A linear regression was performed using rainy days as the independent variable. Cook distances were calculated and interpreted to identify possible outliers, according to Cook and Weisberg (1994).

RESULTS

A total of 2,385 larvae of 12 different species was collected (Table 2). Because Simulium pertinax Kollar, 1832 and S. dekeyseri Shelley & Py-Daniel, 1981 larvae are very morphologically similar, and therefore are difficult to distinguish and S. subnigrum Lutz, 1910 and S. inaequale (Paterson and Shannon 1927) have immature larvae, they
Table 2. Larvae sampled in Tocantins, Brazil during the study (October, 2004 to August, 2005). Number of specimens collected of each species (rows) and locality (columns).

<table>
<thead>
<tr>
<th>Species</th>
<th>Piabanha</th>
<th>Córrego do mato</th>
<th>Ribeirão do lages</th>
<th>Tocantins</th>
<th>All Sites</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. (Chirotolobia) pertinax</em> Kollar, 1832/ <em>S. dekeyseri</em> Shelley &amp; Py-Daniel, 1981</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>10</td>
</tr>
<tr>
<td><em>S. (Chirotolobia) subpallidum</em> Lutz, 1910</td>
<td>147</td>
<td>342</td>
<td>359</td>
<td>19</td>
<td>867</td>
</tr>
<tr>
<td><em>S. (Inaequalium) subnigrum</em> Lutz, 1910 / <em>S. (Inaequalium) inaequale</em> (Paterson &amp; Shannon, 1927)</td>
<td>89</td>
<td>5</td>
<td>0</td>
<td>4</td>
<td>98</td>
</tr>
<tr>
<td><em>S. (Notolepria) cuasiexiguum</em> Shelley et al., 2000</td>
<td>18</td>
<td>0</td>
<td>89</td>
<td>132</td>
<td>239</td>
</tr>
<tr>
<td><em>S. (Psaroniocompsa) incrustatum</em> Lutz, 1910</td>
<td>25</td>
<td>392</td>
<td>0</td>
<td>32</td>
<td>449</td>
</tr>
<tr>
<td><em>S. (Psaroniocompsa) minusculus</em> Lutz, 1910</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>50</td>
<td>54</td>
</tr>
<tr>
<td><em>S. (Psaroniocompsa) quadrifidum</em> Lutz, 1917</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td><em>S. (Psilopelmia) perflavum</em> Roubaud, 1906</td>
<td>0</td>
<td>172</td>
<td>0</td>
<td>0</td>
<td>172</td>
</tr>
<tr>
<td><em>S. (Trichodagmia) guianense</em> Wise, 1911</td>
<td>0</td>
<td>23</td>
<td>0</td>
<td>11</td>
<td>34</td>
</tr>
<tr>
<td><em>S. (Trichodagmia) nigrimanum</em> Macquart, 1838</td>
<td>26</td>
<td>430</td>
<td>0</td>
<td>0</td>
<td>456</td>
</tr>
</tbody>
</table>

Total larvae sampled: 359, 1,364, 448, 248, 2,385

were treated as the same entity when one of these pairs of species was found in a study area. The correlation between the number of larvae sampled and number of species identified was not significant; therefore, we assumed that there was no sampling bias, according to the methodology described in Hamada et al. (2002).

Species abundance varied in space and time. *S. subpallidum* Lutz 1909 was the dominant species in Piabanha in October, December, and June, whereas *S. subnigrum/S. inaequale* dominated in February and *S. nigrimanum* Macquart 1838 dominated in April. The species richness peak at this site was in April (Figure 2).

*S. nigrimanum* was the dominant species in October and February at Córrego do Mato, *S. subpallidum* Lutz 1909 was dominant in December and April, *S. incrustatum* Lutz 1910 was dominant in June, and *S. perflavum* Roubaud 1906 was dominant in August. The species richness peak was also in April (Figure 2).

Only two species occurred at Ribeirão do Lages; *S. subpallidum* was present during all periods, and *S. cuasiexiguum* Shelley et al. 2001 was present only in April, which makes this month the species richness peak at this site also (Figure 2). Larvae were recorded at three times in the Tocantins River (October, December, and June), in the following three distinct pairs of species: *S. incrustatum* and *S. guianense* Wise 1911 in October, *S. subpallidum* and *S. minusculus* Lutz 1910 in December, and *S. cuasiexiguum* and *S. subnigrum/S. inaequale* in June. The diversity peak was in December (Figure 2).

Linear regression indicated a strong significant negative correlation between beta diversity and the number of rainy days per month (F=12.81, P=0.037, R^2=0.8102), whereas the first PC (Figure 3) was precipitation (variance explained: 39.18%), and the second axis was river size (variance explained: 28.61%) (Table 1). The linear regressions performed with PCs showed that *S. subpallidum* positively correlated with precipitation (F=6.2776, P=0.0289, R^2=19.88) but negatively with river size (F=6.2882, P=0.02, R^2=22.23), whereas *S. perflavum* and *S. nigrimanum* negatively correlated with precipitation (F=5.1197, P=0.0338, R^2=18.88) and river size (F=6.6596, P=0.0376, R^2=18.19), respectively. NMDS (Figure 4) pointed toward a marked difference in black fly taxocenoses between the wet and dry seasons.

**DISCUSSION**

The species pairs (*S. pertinax/S. dekeyseri* and *S. subnigrum/S. inaequale*) may have not shown clear mesohabitat feature associations because these are artificial taxonomic entities composed of individual species that are impossible to distinguish morphologically and may have completely different ecological traits, which limits the interpretation of their distributional patterns.

The species richness peaks in April, a transition period between the dry and wet seasons, may represent an intermediate disturbance, and therefore, according to the intermediate disturbance hypothesis (IDH) (Connel 1978), may enhance diversity during this period. Although IDH has recently met criticism (Fox 2013), many authors advocate that even though it is vulnerable to misinterpretations, partly because of the use of different diversity measures (Shel and Burslem 2013), it remains solid when used with species richness, as in the present study (Svensson et al. 2012).

The inverse proportional relationship between the number of rainy days and mean beta diversity value suggests that beta diversity improves when there is little or no precipitation; therefore, dissimilarity among the communities is enhanced, which may explain the differences observed in NMDS between black fly taxocenoses from the dry and wet seasons. The positive association between *S. subpallidum* and precipitation may enhance this explained similarity among sites during the wet season because this species was...
Figure 1. Map of the study area, indicating the four sampling sites: (A) Córrego do Mato. (B) Córrego Piabanha. (C) Ribeirão das Lages. (D) Tocantins.

Figure 2. Larval abundance per site in each sampling date (bars) against the number of rainy days in the month (line): (A) Córrego do Mato. (B) Piabanha. (C) Ribeirão das Lages. (D) Tocantins River.
Figure 3. Principal components analysis showing abiotic factor associations in the black fly species found in the present study. (Mean Hum, monthly mean humidity; 24 h rain, amount of rain during the daytime; Mean Temp, mean temperature of terrestrial habitat; Vel, mean water current velocity; Rainy Days, number of rainy days within a month; Streambed, streambed particle size; Riparian, riparian vegetation characteristics; S. nigri, Simulium nigrimanum; S. subpa, Simulium subpallidum; S. guian, Simulium guianense; S. incrus, Simulium incrustatum; S. perf, Simulium perflavum; S.cuasi, S. cuasiexiguum; S. quadri, S. quadrididum; S. dekey, Simulium dekeyseri/Simulium pertinax; S.min, Simulium minusculum). Axis 1 explains 39.18% of the variation. Axis 2 explains 28.61% of the variation.

Figure 4. Nonmetric multidimensional scaling (NMDS) analysis with the Bray–Curtis index, indicating two distinct groups for the wet and dry seasons.
the most abundant and widely distributed.

Pramual & Wongpakam (2010) also observed marked differences in the black fly community structure between the dry and rainy seasons; however, species richness was significantly higher in the rainy season, when rivers are faster and deeper. They also demonstrated that species predominant during one season substantially decreased in the other, whereas McCreadie et al. (2004) observed that most species present during the wet season were also present during the dry season. Grant et al. (2007) suggested that lotic ecosystems are a dendritic metacommunity, in which networks show a hierarchical branching structure, with mainstreams connected to multiple blind-ended branches (Brown & Swan 2010); therefore, there are no patches because the entire network is a potential habitat (Grant et al. 2007). Therefore, improved precipitation may result in enhanced dispersal (Mathiessen et al. 2010) because of black fly larvae drift through this metacommunity, which reduced beta diversity. Although further studies are necessary, this distinction between dry and wet season communities may be a consistent pattern not only for black fly larvae but for macroinvertebrates of this biome in general.

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