

Bat flies aggregation on *Artibeus planirostris* hosts in the Pantanal floodplain and surrounding plateaus

Research Article

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Author for correspondence:

Alan Eriksson, E-mail: afariksson@hotmail.com

Esther Gonçalves Morimatsu Vieira¹, Erich Fischer², Gustavo Gracioli², Carolina Ferreira Santos², George Camargo³, Maurício Silveira^{3,4} and Alan Eriksson^{3,5}

¹Licenciatura em Ciências Biológicas, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, 79070-900 Campo Grande, Brasil; ²Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, 79070-900 Campo Grande, Brasil; ³Programa de Pós-graduação em Ecologia e Conservação, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, 79070-900 Campo Grande, Brasil; ⁴Programa de Pós-Graduação em Zoologia, Universidade de Brasília, Campus Darcy Ribeiro s/n, Asa Norte, 70910-900 Brasília, Brasil and ⁵Department of Zoology, University of Otago, 340 Great King St, 9016 Dunedin, New Zealand

Abstract

For parasites in natural systems, the most common pattern of spatial distribution is aggregation among hosts. The main causes of such aggregation are variable exposure of hosts to parasites and heterogeneity in host susceptibility. The objective of this study was to determine if there are differences in the aggregation pattern of two species of ectoparasitic flies between the Pantanal and Cerrado regions of Brazil on the bat *Artibeus planirostris*. We collected the ectoparasites from bats captured between 2002 and 2017 with mist nets in 21 sites in the Pantanal and 15 sites in the surrounding plateaus. The results showed that the aggregation of ectoparasitic flies in Pantanal was more pronounced than in Cerrado. The discrepancy aggregation index (D) of the bat fly *Megistopoda aranea* was 0.877 in Pantanal and 0.724 in Cerrado. The D values of *Aspidoptera phyllostomatis* was even higher, with 0.916 and 0.848 in the Pantanal and Cerrado, respectively. Differences in the shelters used may be the main factor shaping variation in aggregation, since the Pantanal does not have rock formations, with only foliage, crowns and hollow tree trunks. These differences likely affect host exposure to the parasites, leading to an increase in parasite aggregation.

Introduction

Parasites often are unevenly distributed across hosts, i.e. few host individuals tend to be highly infested by a given parasite while several other individuals show absence or low levels of infestation (Shaw and Dobson, 1995; Poulin, 2007). Different causes have been proposed to explain the aggregated distribution of parasites across host individuals (Morrill and Forbes, 2012; Poulin, 2013). If different hosts are nearly equally susceptible to be parasitized and exhibit similar ability for removing parasites, then aggregation can arise from differential exposure to the parasites (Poulin, 2007). For instance, it can occur either when only few definitive host individuals prey on intermediate hosts that are highly infested by parasites, or when few hosts use places containing high densities of parasite infective stages (Boag *et al.*, 2001; Hansen *et al.*, 2004; Warburton and Vonhof, 2018). Alternatively, variable susceptibility to acquire or variable ability to remove parasites can additionally contribute to aggregate parasites across hosts (Boag *et al.*, 2001; Poulin, 2007; Morrill and Forbes, 2012). Therefore, addressing factors that potentially affect the exposure of hosts to parasites is central to understand the distribution of parasites in the host populations.

Bat flies (Streblidae) comprise ectoparasites exclusively found on bats, showing high specificity at the host species level (Dick and Patterson, 2006). The knowledge on South American bat flies is mainly restricted to species list and quantitative host parasite associations (Gracioli *et al.*, 2010; Lourenço *et al.*, 2014; Bezerra and Bocchiglieri, 2018). Some studies, however, have showed that infestation by bat flies depends upon the characteristics of the bats' day roosts (ter Hofstede and Fenton, 2005; Patterson *et al.*, 2007). Nonetheless, the potential effects of the roosting environment on bat flies are still poorly understood (Dick and Dittmar, 2014). The larvae develop inside their mothers, which need to leave the host's body for expelling the pre-pupae and attaching them to the wall of the bats' shelters. The pupae must be located on parts of the wall close to bats or bat passages to facilitate host finding by the emerging adults (Overal, 1980; Dittmar *et al.*, 2009). Small day roosts limit the space used by the bats and the size of bat colonies, leading to an aggregation of the pre-pupae in the roosts that potentially increases the effectiveness of emerging adult flies to find a host, thus promoting high infestation of these bat individuals.

The Pantanal is a huge sedimentary floodplain bordered by Cerrado plateaus in the central South American savanna (Nunes da Cunha and Junk, 2010; Pott *et al.*, 2011). The plateaus present rocky formations with caves and crevices that provide bat shelters (Mercante *et al.*, 2011), which are absent in the floodplain. *Artibeus planirostris* is the most abundant fruit-eating bat in both regions

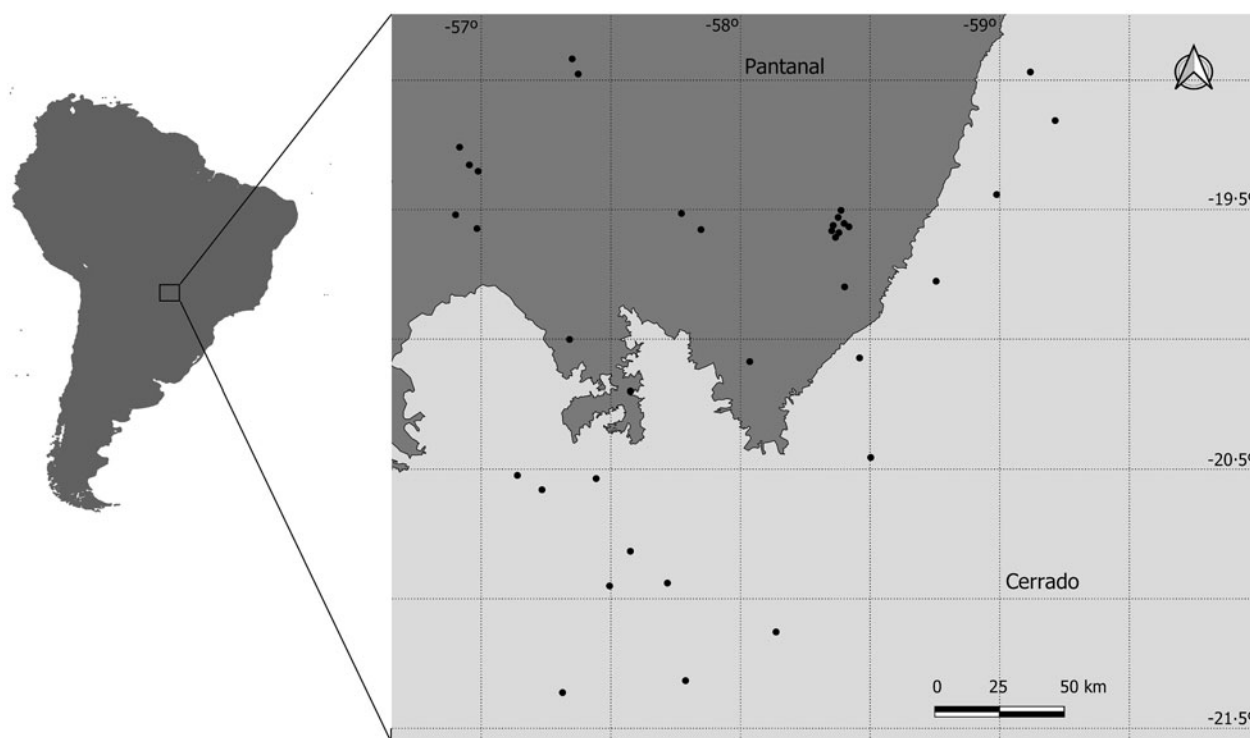


Fig. 1. Study sites (black dots) in the Pantanal floodplain (dark grey) and the Cerrado plateaus (light grey), Mato Grosso do Sul, Brazil.

(Fischer *et al.*, 2018). It uses a variety of roost types, including tree hollows, canopies, and rocky shelters (personal observations; see also Garbino and Tavares, 2018). *Megistopoda aranea* and *Aspidoptera phyllostomatis* flies are the most conspicuous ectoparasites associated with *A. planirostris* in the region (Eriksson *et al.*, 2011; Barbier and Gracioli, 2016). Therefore, the wide occurrence of *A. planirostris* bats in the Pantanal floodplain and Cerrado plateaus represents an opportunity to evaluate the effects of environments with different shelter types on the level of bat fly aggregation. Here, we asked whether the aggregation of bat fly species among *A. planirostris* individuals differs between the Pantanal and Cerrado populations. We hypothesized that bat fly species will present higher aggregation in the Pantanal than in Cerrado, as only small and ephemeral tree hollows are available as shelters for *A. planirostris* in the former, whereas it can additionally use perennial and large shelters, such as caves and rock crevices, in the Cerrado plateaus.

Materials and methods

Study region

We studied bat–bat fly interactions throughout the Miranda and Negro basins, which originate in the Cerrado plateaus and drain to the Pantanal floodplain in Mato Grosso do Sul state, south-western Brazil. Climate is type Aw of Köppen, with the rainy season from October to April and the dry season from May to September (Kottek *et al.*, 2006). The mean annual temperature varies from 23 to 26 °C, and annual precipitation from 1168 to 1477 mm (Hijmans *et al.*, 2005). Typical savannic landscapes, composed of sparse shrubs or trees on grasslands, interspaced with semideciduous forest patches in more humid or riparian sites, predominate in both environments, Pantanal and Cerrado (Pott *et al.*, 2011; Silva and Carlini, 2015; Silveira *et al.*, 2018).

Data collection

We mistnetted bats in 21 sites in the floodplain and 15 sites in the plateaus (Fig. 1) between 2002 and 2017. All sites were

sampled at least one night in the dry and one night in the wet season. Each night, six to ten 12 × 2.6 m mistnets were kept open during 6 h after sunset. In all sites, at least 30 individuals of *A. planirostris* were captured. We considered all captured individuals regardless of age, sex or reproductive stage because effects of these traits on bat flies is unclear (Bertola *et al.*, 2005; Patrício *et al.*, 2016), and because we did not find significant differences in the proportion of the host age, sex or reproductive stage between regions. We inspected every captured *A. planirostris* individuals for ectoparasites, collected the streblids manually or with tweezers, and stored them in microtubes containing 1.5 mL of 70 or 99% alcohol. Bats were then released at the site of capture, except some individuals collected as vouchers and included in the zoological collection of the Universidade Federal de Mato Grosso do Sul (ZUFMS). Collected streblids were identified in the laboratory based on Wenzel (1976) and Guerrero (1995), following the taxonomic classification by Dick and Gracioli (2018); they were also included in the ZUFMS collection.

Data analyses

We calculated the Poulin index of discrepancy (D) to describe the bat fly aggregations, which measures the deviation of a parasite distribution from a theoretically even distribution among host individuals; D ranges from zero to one, indicating no aggregation to highly aggregated distribution (Poulin, 1993, 2007). Different measures of parasite aggregation have similar interpretation and they roughly predict each other (Reiczigel *et al.*, 2019). We choose the index D because it is easy to understand and compute (Poulin, 2007), and appropriate to the statistics available in the Quantitative Parasitology software (QPweb) (Reiczigel *et al.*, 2019), used here for all data analyses. To test for significance of differences of D between the Pantanal and Cerrado, we used a bootstrap approach with 3000 randomizations and accepted significant differences if the 97.5% confidence intervals did not overlap (Reiczigel *et al.*, 2019).

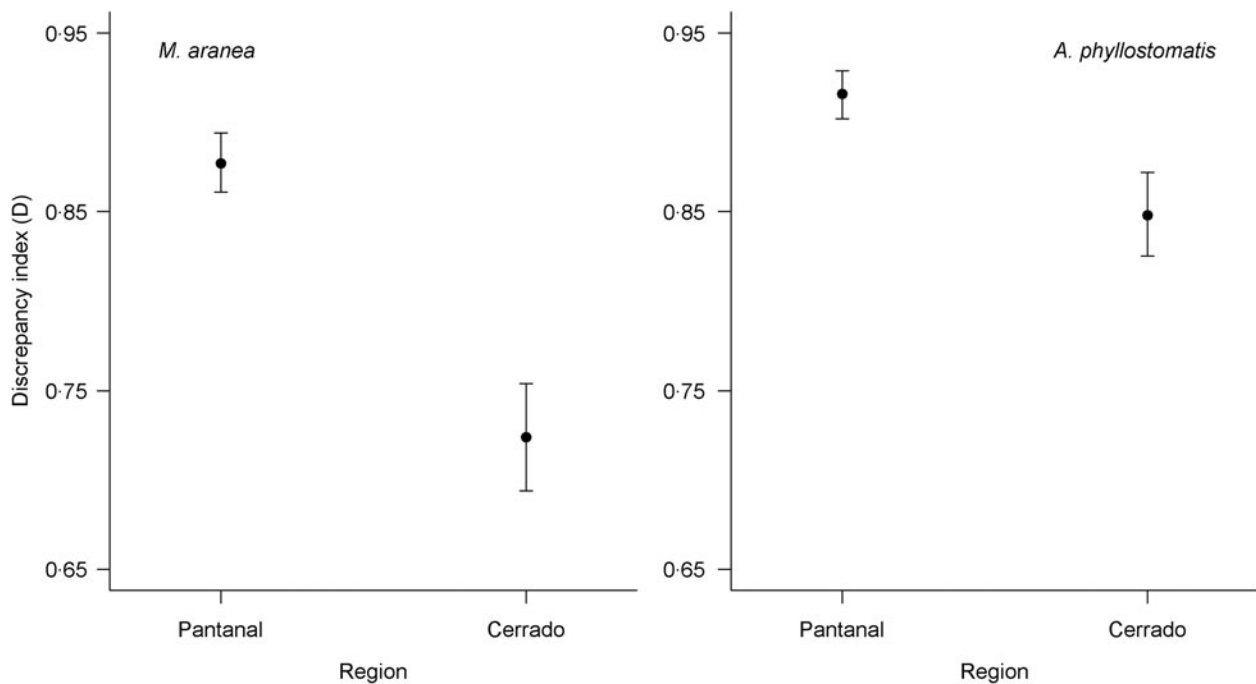


Fig. 2. Poulin index of discrepancy (D) measuring the aggregation of distributions of *Megistopoda aranea* and *Aspidoptera phyllostomatis* bat flies among *Artibeus planirostris* host individuals in the Pantanal floodplain and the Cerrado plateaus, Mato Grosso do Sul, Brazil. Error bars are the 97.5% confidence Intervals ($P < 0.05$).

Results

We sampled 1784 streblid flies from 2497 individuals of *A. planirostris*, consisting of 1698 bats from Pantanal and 799 bats from Cerrado. All bat populations in the 36 sites presented bat flies. *Megistopoda aranea* was almost two times more abundant than *A. phyllostomatis*, with 1117 (494 in Pantanal and 623 in Cerrado) and 667 (327 in Pantanal and 340 in Cerrado) sampled bat flies, respectively. *Megistopoda aranea* and *A. phyllostomatis* showed aggregated distributions in both regions, but their aggregations were higher ($P < 0.05$) in the Pantanal than in Cerrado, and *A. phyllostomatis* showed higher overall aggregation compared to *M. aranea* (Fig. 2). The prevalence of *M. aranea* was 17.3% (s.d. = 10.4%) and 40.8% (s.d. = 9.1%) in the Pantanal and Cerrado, respectively. The prevalence of *A. phyllostomatis* was 13.2% (s.d. = 8.4%) in the Pantanal and 20.7% (s.d. = 8.7%) in the Cerrado.

Discussion

Our results indicate that aggregation of both species of bat flies across *A. planirostris* individuals is higher in the Pantanal floodplain than in the Cerrado plateaus. This outcome supports our initial hypothesis, based on the consideration of regional differences of roost types used by this bat species. Two main reasons for parasite aggregation across host individuals are the exposure and susceptibility of the hosts to parasite infections (Poulin, 2007). Some studies have showed that juvenile or pregnant female bats are more prone to acquire higher infections by bat flies (Rui and Graciolli, 2005; Esbérard *et al.*, 2012). Nonetheless, this increased susceptibility has been not found for *A. planirostris* juveniles or pregnant females (Patrício *et al.*, 2016). We raised that small and ephemeral tree hollows available for *A. planirostris* in the Pantanal could favour an increased aggregation of parasites across host individuals if compared with large and perennial rocky shelters available in the plateaus (Sallun-Filho *et al.*, 2010). Small tree hollows could improve the success of newly emerged flies seeking out a bat host, because the small internal


area of this roost type forces bat individuals to pass close to, or perch on, wall parts where bat fly pupae have been previously deposited. In contrast, large caves and rock fissures allow bats to use variable entrance routes and perching places inside the roost, potentially increasing the uncertainty of encounters of emerging flies with a bat host; actually, bats could actively change their perching location to escape from high infestation (Lewis, 1995).

Differences between Cerrado and Pantanal with regard to numbers and durability of the available roosting places could also affect bat fly aggregation across host individuals. Tree hollows are ephemeral but largely available in the floodplain, which contrasts to rocky shelters in the surrounding plateaus that are perennial but relatively rare. Therefore, *A. planirostris* populations tend to split up into several small groups inhabiting different tree hollows in the floodplain, whereas rocky shelters can concentrate bat individuals into few and large groups in the plateaus (Díaz and Linares García, 2012; Breviglieri and Uieda, 2014; Cordero-Schmidt *et al.*, 2016). Low durability of bats' roosting places can reduce bat fly prevalence (Patterson *et al.*, 2007), as we found for *M. aranea* and *A. phyllostomatis* in the Pantanal. Thus, few bat groups in tree hollows would be infested and all individuals in these groups would be consistently parasitized due to the confined space in which they roost. If so, bat fly aggregation should be high because only a small fraction of host individuals is continuously infested. On the other hand, large bat groups sharing perennial rocky shelters in the Cerrado plateaus could favour a high prevalence and low aggregation of bat flies among hosts.

The prevalence of *M. aranea* was higher than that of *A. phyllostomatis* in both regions, Pantanal and Cerrado, a pattern already reported (Eriksson *et al.*, 2011; Barbier and Graciolli, 2016; Dornelles *et al.*, 2017). Although they occupy different portions of the host body, competition has been evidenced between these bat fly species (Hiller *et al.*, 2018, but see Presley, 2011). The highest prevalence of *M. aranea* in both of our studied regions indicates that *M. aranea* is a more successful competitor than *A. phyllostomatis*. Different patterns of pupae deposition could be another cause of differences in prevalence between

these fly species on *Artibeus* hosts (Pilosof *et al.*, 2012; Hiller *et al.*, 2018). We suggest that *A. phyllostomatis* pupae are deposited in more exposed areas of the bat roosts and thus subjected to external climatic conditions, decreasing the survival rate of pupae and consequently decreasing the availability of individuals to infect bats.

The availability of caves and rock crevices in the Cerrado and the absence of such roosting places in the Pantanal provide a potential explanation for differences of bat fly aggregation patterns on *A. planirostris* individuals. However, further studies on roost types and numbers of bats per roost are required to support that. Although *A. planirostris* uses a variety of roost types (Garbino and Tavares, 2018), there are no data on the use of roost sites in our study Cerrado plateaus. It is usually assumed that differences in bat fly abundance result from the type or condition of host's roosts (ter Hofstede and Fenton, 2005; Patterson *et al.*, 2007; Pilosof *et al.*, 2012; Bolívar-Cimé *et al.*, 2018; Hiller *et al.*, 2018). Such explanation makes sense since the bat fly pupal stage is decoupled from the bats, nevertheless the literature on pupae deposition is scarce (Overal, 1980; Fritz, 1983; Dittmar *et al.*, 2009). Further studies on the patterns of pupal deposition in different roosts, as well as on the biotic and abiotic factors affecting pupae are important to understanding the distribution of bat flies across bat host individuals.

Author ORCIDs.  Erich Fischer, 0000-0001-8722-9876; Alan Eriksson, 0000-0003-1857-7935.

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Conflict of interest. None.

Ethical standards. Bat captures were conducted under legal authorization of Brazilian Ministry of the Environment MMA/ ICMBio permit numbers, 10303-1 and 41652-1.

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