



TEMPORAL DYNAMICS IN PANTANAL HUMMINGBIRD ASSEMBLAGES IS TRIGGERED BY FLOOD PULSE

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Abstract · Hummingbirds (Trochilidae) are highly specialized New World birds that depend on nectar as their major food source. In response to seasonal food limitations, many trochilids develop dispersal and long-distance migration patterns, but these patterns are understudied for many continental South American species. In this study, conducted in the Brazilian Pantanal, we investigated the movement patterns of hummingbirds in a highly variable environment, where an annual flood pulse leads to four distinctive seasonal periods (high water, receding water, dry period, and rising water). Our objective was to verify how these four periods affected the hummingbird community according to habitat occupation in savannas or forests. This study was conducted in the northeastern Pantanal of Mato Grosso, Brazil (16° 39'S, 56°47'W, 119–131 m a.s.l.), covering two annual inundation periods (2014–2016). Data were collected using mist net sampling. Two migrant and seven resident species were identified. The results indicated significant differences in hummingbird species richness and abundance between habitats; savanna habitats were the richest habitats during rainy seasons (rising and high water). Higher hummingbird abundance in these seasonal periods was seemingly related to higher food availability since these seasons corresponded to the main flowering period of ornithophilous plants and other angiosperms.

Resumo · Impacto do pulso de inundação sobre a dinâmica temporal das assembleias de beija-flores do Pantanal Mato-Grossense

Os beija-flores são aves do Novo Mundo, altamente especializadas, que dependem do néctar como principal fonte de alimento. Em resposta às limitações alimentares sazonais, muitos trochilídeos desenvolveram padrões de dispersão, e até mesmo de migração por longas distâncias, porém, estes fenômenos ainda são pouco estudados para muitas espécies continentais da América do Sul. Neste estudo, conduzido no Pantanal de Mato Grosso, foram investigados os padrões de movimentação de espécies de beija-flores em um ambiente altamente variável, em que o pulso de inundação anual caracteriza-se por quatro períodos sazonais distintos (cheia, vazante, seca, enchente). O objetivo deste estudo foi verificar como a comunidade de beija-flores foi afetada por estes quatro períodos de acordo com a ocupação do habitat em savanas ou florestas. Para este estudo, realizado no nordeste do Pantanal de Mato Grosso, Brasil (16° 39'S, 56° 47'W, 119-131 metros acima do nível do mar), foram analisados dois períodos anuais de inundação (2014-2016), empregando-se redes de neblina para a coleta dos dados. Dentre as nove espécies identificadas, duas são migrantes e sete residentes. Os resultados indicaram uma diferença significativa na riqueza e abundância das espécies de beija-flores entre os habitats analisados, e as savanas apresentaram maior riqueza durante as estações chuvosas (enchente e cheia). A maior abundância de beija-flores nesses períodos sazonais aparentemente está relacionada à maior disponibilidade de alimentos, uma vez que essas estações correspondem aos principais períodos de floração das plantas ornitófilas e outras angiospermas.

Keywords: *Hummingbird dispersion · Hummingbird migration · Resource availability · Seasonality*

INTRODUCTION

The Pantanal is the world's largest seasonally flooded wetland, with an annual hydrological cycle (Junk & Da Silva 2000, Junk et al. 2006, 2011) that progressed at the end of the Tertiary (Almeida 1945, Beurlen 1956) and a mosaic of phytophysiognomies characterizes it. These are influenced by biomes such as the Cerrado, the Chaco, and the Amazon Rainforest (Nunes da Cunha et al. 2007). The Pantanal stands out for its high biodiversity, especially of birds, with c. 450 species (among these, 21 hummingbird



species) comprising resident and migratory taxa from different parts of the Nearctic, Neotropic, and Austral Regions (Hagan & Johnson 1992, Jahn et al. 2004, Gwynne et al. 2010).

Most avian species in the Pantanal respond to predictive seasonality by dispersal and regional or intercontinental migration in search of food (Antas 1994, Antas & Palo 2004, Nunes & Tomas 2004). Species dependent on water depending on the flood pulse to reproduce (e.g., waders, ducks, kingfishers; Antas & Palo 2004). Terrestrial birds also show adaptations in the timing of their breeding cycles to seasonal climatic conditions and food availability (Ragusa-Netto 2004, 2005, 2006, 2007, Newton 2008). The seasonal predictive hydrological cycle in the Pantanal influences ecological processes such as the structure of the landscape, the trophic state, and the availability of food resources (Figueira et al. 2006). These characteristics strongly impact organisms' diversity, abundance, reproduction, and migration (Junk & Da Silva 2000). As Junk et al. (2006) pointed out, the seasonality of food resources is one of the main reasons for the Pantanal's high diversity of organisms, particularly birds (Figueira et al. 2006, Signor & Pinho 2011).

Food availability is a determining factor in avian dispersal and migration. Hummingbirds are nectarivorous and dependent on the flowering of ornithophilous and nonornithophilous angiosperms (Levey & Stiles 1992, Schuchmann 1999, Newton 2007, Faaborg et al. 2010, Rodrigues & Araujo 2011, McKinney et al. 2012). Most trochilids are generalists, capable of exploiting their resources in different habitats and visiting different flowers (Borgella et al. 2001, Temeles et al. 2002, Araujo & Sazima 2003). However, their presence tends to vary according to local climatic conditions and the availability, diversity, and abundance of nectar resources (Schuchmann 1996, Varassin & Sazima 2000, Malizia 2001, Cotton 2007, Abrahamczyk & Kessler 2010, Rodrigues & Rodrigues 2015).

Hummingbirds are capable of long-distance flights (Rappole & Schuchmann 2003). The main reason that leads species to carry out any movement is the search for survival resources, and their movements can be classified into two main categories: dispersion and migration (Boyle 2018). Dispersion involves the movement of young individuals to the natal area or movement without a specific destination, while migration is portrayed as the periodical movement of individuals to specific destinations (Berthold 1993, Schuchmann 1999, Rappole & Schuchmann 2003).

This study aimed to verify hummingbird movements and species distributions over different habitats and seasonal periods in the northeastern Pantanal. Our hypothesis was that some hummingbird species would occur only in certain periods and places, and their abundance would vary since the food resource availability may change in different seasonal periods. We expected a higher richness and abundance of trochilids to occur during the high-water periods since these periods may present more flowering ornithophilous angiosperms species.

METHODS

Study area. Our study was carried out at the Serviço Social do Comércio (SESC) Baía das Pedras, one of the units of the SESC Pantanal Ecological Resort, in the Poconé municipality in the northeastern Pantanal of Mato Grosso State, Brazil (16°39'S, 56°47'W). The site is seasonally inundated and lies within a privately protected area of c. 4200 ha within the Cuiabá River, one of the main tributaries of the Paraguay River within the Pantanal. The regional climate is tropical, with an average annual temperature of approximately 24°C and mean annual rainfall ranging from 1000 to 1500 mm (Junk et al. 2006).

Seasonality. Yearly, the Pantanal changes due to flooding by the Paraguay River and its tributaries, local precipitation events, and/or water seepage connections (Junk & Da Silva 2000, Junk et al. 2011). This annual cycle leads to four seasonal episodes: a dry period from July to September caused by the strong hydric deficit; a rising water period from October to December, starting with rain; a high water period (or wet period), when inundations peak from January to March; and a receding period when water declines from April to June (Heckman 1998). The level of the flood pulse may vary annually depending on the volume of precipitation surrounding the Pantanal basin.

Sampling design and data collection. We collected data from July 2014 to July 2016 during two annual hydrological cycles. Our study area encompasses a mosaic of different forest formations (e.g., monodominant forests, semideciduous forests) and savannas (e.g., bush savanna, low tree and shrub savanna, and steppe savanna), areas with significant variations in floristic components and structural vegetation (De Deus et al. 2020). Eight sampling sites were established in the landscape separated by at least 1 km. We selected four savanna sites and four forest sites to estimate the variation in vegetation components. The former was characterized by scattered trees and a large proportion of grassland and shrubs. In contrast, forest sites were characterized by a high proportion of large trees that formed a mostly continuous canopy structure. Forests were sampled 26 times, and savannas were sampled 25 times over the 24 months of data collection.

Hummingbirds. We used mist nets to estimate hummingbird species abundance (Bibby et al. 2000) 9 m long by 2.7 m high and 20 mm mesh. The nets were opened for five hours starting at sunrise (6:00 h) and two hours before sunset (15:00 to 17:00 h), which were periods of high bird activity. At each of the eight sampling sites, five nets were run at two different points 200 to 250 m apart for three consecutive days. The hummingbirds captured were identified following the South American Classification Committee (Remsen et al. 2023). Hummingbird species captured in all seasonal periods at any of the four sites were considered residents, and those observed only in two seasonal periods were considered migrant birds.

Statistical analyses. To evaluate the effects of seasonality and habitat type on variation in the abundance of humming-

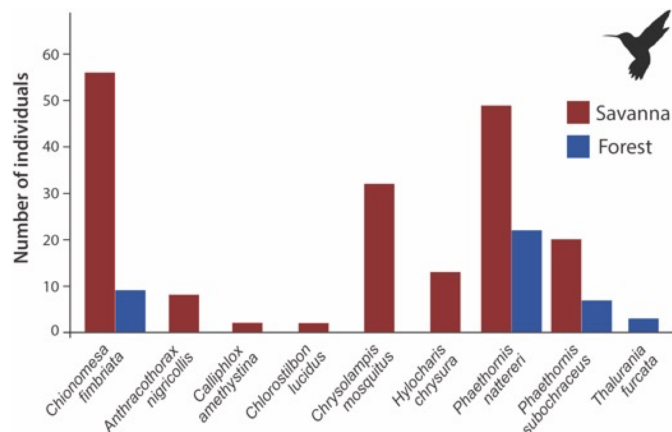


Figure 1. Total hummingbird individuals of each species captured over two annual cycles in savanna and forest in the Pantanal of Poconé, MT, Brazil.

bird species, we used permutational multivariate analysis of variance (PERMANOVA). The abundance of each hummingbird species was compared between sampling sites within habitat types (savanna and forest) and between sampling sites within aquatic and terrestrial periods (rising water, high water, receding water, and dry period). PERMANOVA was run with 9999 permutations using the Bray–Curtis dissimilarity measurement to calculate the pseudo-F that shows differences in dissimilarity between treatments (Anderson & Walsh 2013). The level of significance was $p < 0.05$.

RESULTS

Hummingbird community structure and composition. Over two annual cycles (2014–2016), we captured 223 individuals from eight genera and nine species. The most abundant species were *Phaethornis nattereri* (71 ind.), *Chionomesa fimbriata* (65 ind.), and *Chrysolampis mosquitus* (32 ind.) (Figure 1). We captured 182 individuals of eight species in savannas and 41 individuals of four species in forests. *Anthracothorax nigricollis*, *Calliphlox amethystina*, *Chlorostilbon lucidus*, *C. mosquitus*, and *Hylocharis chrysura* were exclusive to savanna habitats, while *Thalurania furcata* was captured only in forest habitats (Figure 1). Savannas had the highest estimated rich-

ness and abundance of hummingbird species (Figure 2). A general trend observed during the two annual cycles was an increase in the abundance and number of hummingbird species during the rising water and high water periods and a decrease in the receding water and dry period, with only birds of two hummingbird species captured in both annual cycles (Figures 3 and 4). In both years, more species were found in the rising and high-water periods (Figure 4).

We found a significant difference in hummingbird species richness between forest and savanna habitats in both years ($F = 6.275$, $p = 0.002$) and a marginal trend between the seasonal periods ($F = 2.601$, $p = 0.057$). The differences between years did not affect hummingbird richness ($F = 0.922$, $p = 0.421$).

Thalurania furcata, *C. mosquitus*, *C. amethystina*, and *A. nigricollis* were observed only in the rising and high water periods (Figures 3 and 4). *Hylocharis chrysura* and *C. lucidus* were observed in the high and receding water periods (Figures 3 and 4). *Phaethornis subochraceus* was observed in three periods (rising water, high water, and receding water) (Figures 3 and 4). *Phaethornis nattereri* and *C. fimbriata* were recorded in all seasonal periods and were also the most abundant species (Figures 3 and 4).

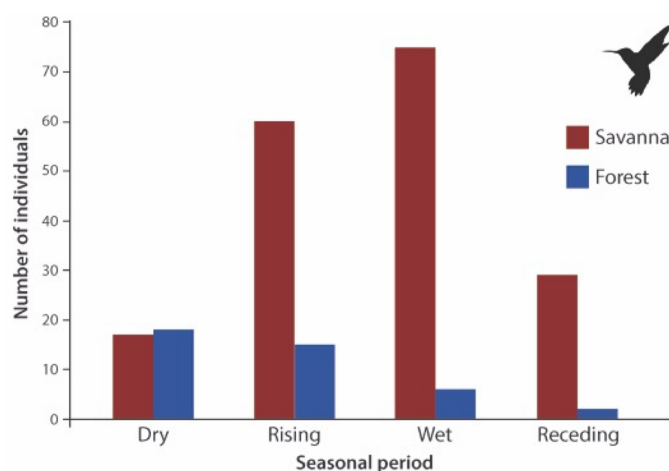


Figure 2. Total hummingbird individuals captured over two annual cycles (2014–2016) in each seasonal period and each forest and savanna in the Pantanal of Poconé, MT, Brazil.

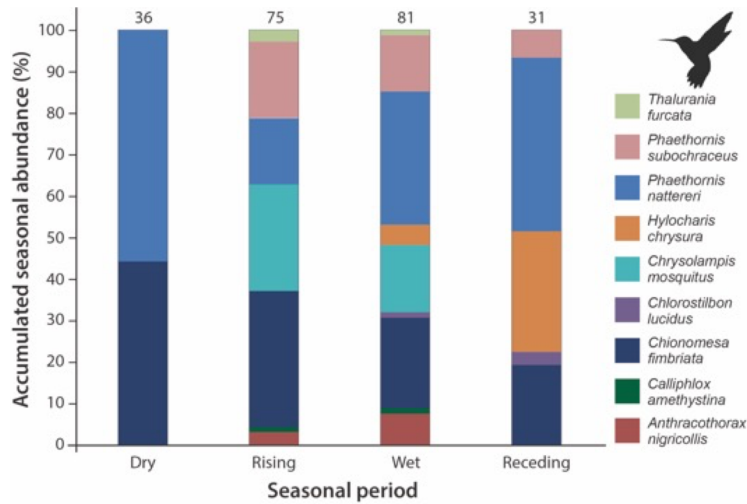


Figure 3. Percentage of hummingbirds captured over two annual cycles (2014–2016) during each seasonal period in the Pantanal of Poconé, MT, Brazil. Column numbers indicate the total number of individuals captured in each period.

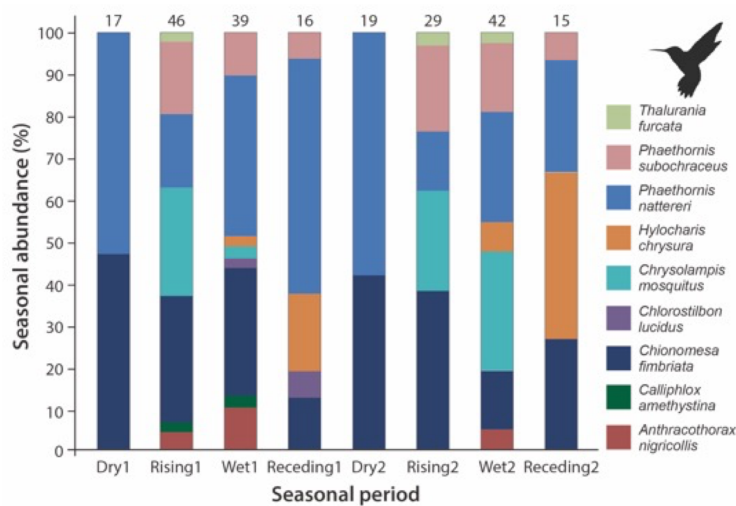


Figure 4. Percentage of hummingbirds captured over each successive seasonal period in each sampling year in the Pantanal of Poconé, MT, Brazil. The sequence of seasonal periods was: Dry 1 and Rising 1 (2014); Wet 1, Receding 1, Dry 2, and Rising 2 (2015); and Wet 2 and Receding 2 (2016).

DISCUSSION

Our study shows that two trochilids, *P. nattereri* and *C. fimbriata*, were residents of the northeastern Pantanal since they were recorded year-round. The continuous presence of those species correlates with the occurrence of ornithophilous angiosperm species throughout the year, with slight seasonal variation (Sazima et al. 1996, Rodrigues & Rodrigues 2015), as well as with nonornithophilous species that are also visited by hummingbirds (Araujo and Sazima 2003). At our study site, four species were found only in the rising and high water periods (*T. furcata*, *C. mosquitus*, *C. amethystina*, and *A. nigricollis*), while two species were recorded only in the high water and receding water periods (*H. chrysura* and *C. lucidus*). The occurrence of these species may be related to climatic events that triggered the onset of flowering in certain angiosperms.

Two hummingbird species were considered migrants to the Pantanal: *A. nigricollis* and *C. mosquitus* (Nunes & Tomas 2004). According to the literature, *A. nigricollis* is a migrant from Central America and northern South America. *Chrysolampis mosquitus* is considered a migrant with annual move-

ments to and from Venezuela (Gran Sabana), Colombia (Cauca Valley), and Panama (Schuchmann & Kirwan 2020, Nunes & Tomas 2004). Both species have been found in forested habitats (Nunes & Tomas 2004); in this study, *C. mosquitus* was abundant and found only in savanna areas. A preference by *C. mosquitus* for savanna habitat was also observed in northern Minas Gerais, Brazil (Schuchmann & Kirwan 2020). The occurrence of *C. mosquitus* in the Pantanal may be related to the blooming of *Bromelia balansae*, since *C. mosquitus* was frequently observed around stands of this terrestrial bromeliad.

Several factors affect the movement of hummingbird species; in general, they migrate or disperse according to the availability of food resources, whether one or more specific plant species (López-Segoviano (2018) for *Selasphorus rufus* and *Amazilia beryllina* in temperate forests of México). This type of movement toward places where plant species are in flower agrees with the results of other studies (Hobson et al. 2003, Tinoco et al. 2009, Fraser et al. 2010, López-Segoviano et al. 2021). In our study, the higher richness and abundance of hummingbirds in savanna habitats during the rising water and high-water periods seemingly coincided with the flowering of ornithophilous species as found in other studies, such as

Palicourea sp. (Rubiaceae), *Helicteres* sp. (Malvaceae), and *Bromelia balansae* (Bromeliaceae) (Stiles 1975, Arizmendi & Ornelas 1990, Araujo 1996, Buzato et al. 2000, Araujo & Sazima 2003). Araujo & Sazima (2003) made similar observations in the southern Pantanal, where ornithophilous angiosperms were of a higher density and experienced peak flowering during the rainy seasons. In general, hummingbird species richness is higher in environments with a greater diversity of nectar-rich food resources compared to habitats dominated by single plant family representatives, e.g., Vochysiaceae, as in the Pantanal monodominant forests (Rodrigues & Rodrigues 2015).

Some hummingbird taxa that are not considered migrants to the Pantanal region were nonetheless captured only in specific seasonal periods: *T. furcata* and *C. amethystina* (rising and high water), *H. chrysurus* and *C. lucidus* (high and receding water), and *Phaethornis subochraceus* (rising, high, and receding water). Although these species are not migratory, their occurrence was clearly delimited by time, and they preferred periods with higher humidity.

Phaethornis nattereri and *C. fimbriata* were captured and observed in all seasonal periods over the two annual cycles, indicating generalized behavior and the use of ornithophilous and nonornithophilous angiosperms. The foraging behavior of floral types other than ornithophilous flower resources has been observed in different tropical and montane environments, including the dry period on savannas (Araujo & Sazima 2003, Abrahamczyk & Kessler 2010, Araujo et al. 2013, Maruyama et al. 2013). In the Pantanal, we observed two behaviors among hummingbirds. Some species occurred in periods propitious for ornithophilous plants (personal field observation). At the same time, generalist hummingbirds showed no preference between high water and dry periods, consequently feeding on different kinds of flowers.

Both the type of habitat and the seasonal period affected the hummingbird richness in the Pantanal, while in other regions of Brazil, significant changes were verified only when considering resource availability in different habitats (Rodrigues & Rodrigues 2015). In our study, the greater abundance of hummingbird species in the rising and high-water periods is congruent with other regions of Brazil and beyond, where higher hummingbird richness was also observed in high water periods (Arizmendi & Ornelas 1990, Sazima et al. 1996, Piratelli & Pereira 2002, Araujo & Sazima 2003, Rebellato & Nunes da Cunha 2005). In summary, a preference for and fluctuation of some resources in the environment, together with the migratory behavior observed in some hummingbirds, explains the distribution and occurrence of trochilids over the different seasonal periods in the Pantanal (Signor & Pinho 2011, Pinho et al. 2017).

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