

RESEARCH ARTICLE

Richness, abundance and microhabitat use by Ardeidae (Aves: Pelecaniformes) during one seasonal cycle in the floodplain lakes of the lower Amazon River

 Giulianne Sampaio Ferreira¹, Danilo Augusto Almeida dos Santos¹, Edson Varga Lopes^{1,2}

¹Programa de Pós-Graduação em Recursos Aquáticos Continentais Amazônicos, Universidade Federal do Oeste do Pará. Rua Vera Paz, 68035-110 Santarém, PA, Brazil.

²Instituto de Biodiversidade e Florestas, Universidade Federal do Oeste do Pará. Rua Vera Paz, 68035-110 Santarém, PA, Brazil.

Corresponding author: Giulianne Sampaio Ferreira (giulya_sampaio@hotmail.com)

<http://zoobank.org/FCF9538B-4804-4920-8450-2139F52C72D4>

ABSTRACT. The Amazon floodplains become periodically submerged as result of seasonal changes in the water levels throughout the year. These changes influence the availability of microhabitats and consequently the abundance of organisms in these ecosystems. In this study we investigated 1) how changes in the water level affect the richness and abundance of ardeid birds in the lowland floodplain lakes of the lower Amazon River, and 2) the microhabitats used by these birds throughout the seasonal cycle. Ten lakes were surveyed at each of the four phases of the seasonal cycle. In total, 3,280 individuals of 11 species were recorded. Of these, eight species occurred in the four phases, and three were observed in one or two phases. In the analysis including the entire family, there were more individuals in the phase with waters at lowest level and less in the phase that the water level was lowering. Many species were present throughout the seasonal cycle, suggesting that they might be resident species. However, their abundance varied throughout the cycle, suggesting that parts of their populations temporarily migrate elsewhere. The microhabitat that was most commonly used by most species at all phases of the seasonal cycle, with the exceptions noted below, was “aquatic macrophytes”, suggesting that ardeid birds have a strong preference for this kind of habitat. Three species – *Egretta caerulea* (Linnaeus, 1758), *Nycticorax nycticorax* (Linnaeus, 1758) and *Bubulcus ibis* (Linnaeus, 1758) – preferred other microhabitats at some phase of their seasonal cycle. The present study shows that the floodplain lakes of the lower Amazon River are richer in ardeid bird species than other areas of the Amazon biome and other biomes in Brazil. The fact that we found rare species in our study and that they depend on aquatic macrophytes demonstrates the importance of conserving the floodplain lakes of the lower Amazon River.

KEY WORDS. Amazonian, aquatic macrophytes, ecological partitioning, waterbirds, wetlands.

INTRODUCTION

Since Huchtnson (1957) proposed the concept of ecological niche, our understanding of biodiversity and how species are distributed in an environment have evolved significantly. For instance, narrow species' niches are often associated with higher species richness locality. This is particularly noteworthy in the tropics and decreases North and Southwards, resulting in a latitudinal gradient in species richness (e.g., Rohde 1992, Fine 2015, Willig and Presley 2018).

The spacial distribution of species within habitats reflects their ecological partitioning, and the number of habitats used

by each species reflects their degree of specialization in habitat use (Stotz et al. 1996). Most ardeid birds are associated with wetlands (Sick 1997, Accordi 2010). However, the use of habitats by these birds can vary considerably according to their degree of specialization (Dimalexis et al. 1997, Bancroft et al. 2002, Isacch and Martínez 2003). While some species use various types of habitats, others are strongly associated with a particular habitat or microhabitat (Accordi and Hartz 2006, Gimenes and Anjos 2011, Alves et al. 2012, Pinto et al. 2013).

Some wetlands change considerably throughout a year (Sioli 1985). For example, Amazon floodplains are strongly influenced by the flood pulse and become seasonally flooded as a

consequence of river overflows (Sioli 1985, Piedade 1995, Junk et al. 1989, Fraxe et al. 2007, Ribeiro 2007). A seasonal cycle in these floodplains includes four distinct phases: 1) rising – elevation of water level, 2) peak-flood – sustained water level acme, 3) ebb – descent of water level, and 4) dry – waters at lowest level (Fraxe et al. 2007). This variation in water levels drastically alters the landscape (Piedade 1995), possibly influencing the availability of suitable habitats for ardeid birds. These birds, in turn, may vary in their response to changes in the floodplain landscape, depending on the breadth of their ecological niche and/or the availability of similar habitats at each stage of the seasonal cycle (structure, food availability, refuge conditions) (Figueira et al. 2006). If the habitat of a highly specialized species disappears at some stage of the seasonal cycle, such species is expected to move or migrate elsewhere (Thompson and Townsend 2006), while more generalist species are more likely to find available habitats locally year-round (Stotz et al. 1996, Petermann 1997).

There are numerous lakes in Amazon floodplains (Piedade 1995). These lakes are extremely important for organisms associated with wetlands, since they generally do not dry out completely during the dry season of the flood cycle, with waters at lowest level (Fraxe et al. 2007). Corroborating this idea, several studies have shown that lakes in periodically flooded areas concentrate food resources for waterbirds during the driest periods of the year (e.g., Antas 1994, Stotz et al. 1996, Silva et al. 2002, Figueira et al. 2006).

Even though both ardeid birds and floodplains are relatively common in the Amazon (Hancock and Elliott 1978, Cintra et al. 2007), information on how these birds use their habitat throughout the year is scarce. In this study we investigate the variations in the abundance of Ardeid bird species and their habitat use in floodplain lakes throughout a seasonal cycle.

Considering that these birds are influenced by the dynamics of the flood pulses of the floodplains, we aimed to answer the following questions: 1) which species are present throughout the year? 2) In which phase of the seasonal cycle is each species more abundant? 3) which microhabitats are explored by ardeid birds in the floodplain lakes of the lower Amazon River? 4) Are microhabitats used by these birds the same at each stage of the seasonal cycle? Upon answering these questions, we hope to contribute to the conservation of the various species and their ecosystems in the Amazon floodplains.

MATERIAL AND METHODS

This study was carried out in a lowland area of the lower Amazon River, municipality of Santarém, western state of Pará, settlement of Santa Maria do Tapará (2°21'22.25"S; 54°34'15.79"W; Fig. 1). The climate is hot and humid, with average annual temperature ranging from 25 to 28°C and average annual rainfall 1,920 mm. The region is characterized by a period of more rain between December and May, and a drier period from June to November (INMET 2013).

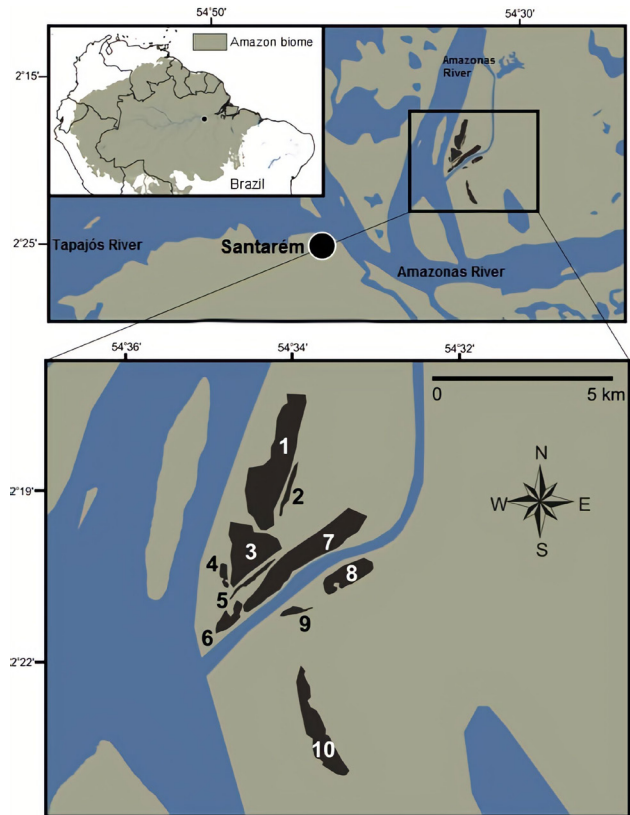


Figure 1. Map of the study area at the low Amazon River. It shows the location of the city of Santarém, at the confluence of the rivers Tapajós and Amazonas, and an enlargement of the study area, highlighting the 10 lakes selected for the survey.

We selected ten lakes for this study (Table 1). All of them are connected to the Amazon River when the water level is high, but only a few remain connected to rivers or canals when the water is at lowest level. The vegetation around the lakes is composed of ‘várzea’ forest (a type of forest typical of floodplains in the Amazon), agglomerations of plants of *Cecropia* (locally known as ‘embaubal’), and natural fields. In the lakes there are aquatic macrophytes such as *Eichhornia crassipes* (Mart) Solms, 1883 (Pontederiaceae), *Montrichardia linifera* (Arruda) Schott, 1854 (Araceae) and *Victoria amazonica* (Poepp.) J.C. Sowerby (Nymphaeaceae).

Data collection followed the line transect method in Bibby et al. (1992). During rising, peak-flood, and ebb phases we used a small wooden boat to transect each lake, about 20 m from the margin. The boat’s engine, known locally as ‘rabeta’, travels at an average speed of approximately 10 km/h. During the dry season, with lowest water levels, access to most lakes using boats became very difficult. Consequently, during this period, the transect was covered by foot, along the banks of the lake, at an average speed of 1 km/h. We sampled three lakes per day, starting at 07:00 am

and ending at around 11:00 am. Between July 2013 and May 2014 (an entire seasonal cycle), each lake was sampled twice at each phase of the cycle, totaling eight samplings at each lake.

The species were identified through direct visual contact or with binoculars (8 x 42). We recorded all individuals of Ardeidae visualized during each sampling. Individuals flying over the lake were not counted, and we tried to avoid registering the same individual more than once. Thus, in addition to documenting each species, we also estimated their abundance.

Table 1. Geographical coordinates and size of the ten lakes selected for this study. The lakes were measured during the phase with waters at lowest level. Calculations done in the program GEPATH 1.4.6.

| Lake | Coordinates | Area (km ²) |
|---------------|-----------------------------|-------------------------|
| Aninga | 2°19'15.42"S; 54°34'0.91"W | 8.12 |
| Botal | 2°19'17.76"S; 54°33'41.30"W | 2.72 |
| Caiçara | 2°20'3.17"S; 54°34'10.78"W | 4.88 |
| Espurú | 2°20'27.26"S; 54°34'33.46"W | 1.73 |
| Figueiredo | 2°21'0.47"S; 54°34'23.87"W | 2.24 |
| Pitomba | 2°20'29.34"S; 54°34'11.19"W | 3.36 |
| Poço | 2°20'54.73"S; 54°33'31.54"W | 1.88 |
| Pucu | 2°20'27.89"S; 54°33'48.65"W | 8.27 |
| Purus | 2°22'35.35"S; 54°33'18.18"W | 7.06 |
| São Francisco | 2°20'29.75"S; 54°32'51.27"W | 3.29 |

We characterized the use of microhabitat for each individual or flock (three or more individuals) registered at a lake or around it, up to 20 m from the bank. We considered the microhabitat exploited by a bird as being the predominant habitat within an estimated radius of five meters around that bird at the moment of the record (Lopes et al. 2006). We created microhabitat categories based on Alves et al. (2012), to standardize data collection, as follows: 1) Tree vegetation – woody plants three meters in height, or more, isolated or in clusters; 2) Shrub vegetation – woody plants less than three meters high; 3) Grass – herbaceous undergrowth, few centimeters in height; 4) Bare margin – area around lakes, without vegetation cover; 5) Lake perch – structure placed at the interior of the lake, such as wooden sticks to hold small boats; 6) Marginal perch – similar to the previous one, but the structure was fixed at the edge of the lake, out of the water; 7) Aquatic macrophytes – aquatic plants inside the lake; 8) Coastal zone – within the water, from the margin up to five meters; 9) Limnetic zone – in the water, beginning five meters from the shore. This last category was included because, during periods when the water level was at its lowest, the lakes became very shallow and the birds were able to enter the them.

To verify if there was variation in species' abundance among the four phases of the seasonal cycle, we used the non-parametric statistical test Chi-square (χ^2). Since two samplings were carried out in each phase, we analyzed, for each species, the

sample encompassing the largest number of recorded individuals. This analysis was done in the STATISTICA 7.0 program (Statsoft 2004) when the frequencies recorded were higher than five (Fowler and Cohen 1995), at significance level of 5% ($\alpha = 0.05$).

In order to determine the preference of the species for a specific microhabitat at each stage of the seasonal cycle, we used a simple correspondence analysis (CA) according to Legendre and Legendre (1998). This graphical analysis was developed to represent the association between rows and columns of a contingency table. The proximity of the points referring to the row and the column indicates an association between these variables and their distancing represents a repulsion (Gonçalves and Santos 2009). The CA was carried out in the Paleontological Statistics-PAST program (Hammer et al. 2001). We performed ordinations between the species studied and the categories of microhabitats considered. For this analysis we constructed matrices with the percentage of occurrence of each species in each microhabitat. We adopted this procedure for the four phases of the seasonal cycle, and included only those species for which we had five or more records. Thus, a species may have been analyzed for one phase but not for another when records of it were too few or lacking.

RESULTS

Considering all phases of the seasonal cycle, we recorded 3,280 individuals from 11 species of Ardeidae (Table 2). *Ardea alba* Linnaeus, 1758 was the most abundant species, corresponding to 39.8% of the total records (Table 2). *Bubulcus ibis* (Linnaeus, 1758) and *Egretta thula* (Molina, 1782) were also relatively abundant (24.7% and 19.6% of the total records, respectively). Less than 200 individuals were recorded for each of the other species during the seasonal cycle (Table 2). *Cochlearius cochlearius* (Linnaeus, 1766), *Ixobrychus exilis* (Gmelin, 1789) and *Pilherodius pileatus* (Boddaert, 1783) were not included in the analyzes of abundance and microhabitat use because they were very low in numbers, and nocturnal habitat of the first species mentioned.

The highest and the lowest abundance of ardeid individuals occurred when the water was in the lowest levels and when the water level was lowering (dry and ebb phases), respectively (Table 2). Eight of the 11 species recorded were present in the four phases of the seasonal cycle, six of which significantly varied in numbers throughout the seasonal phases. *Ardea alba*, *Butorides striata* (Linnaeus, 1758), *Egretta caerulea* (Linnaeus, 1758), *E. thula* and *Nycticorax nycticorax* (Linnaeus, 1758) were more abundant in the phase with lowest water levels. In contrast, *B. ibis* was more abundant in the peak-flood phase. The abundance of two species, *Tigrisoma lineatum* (Boddaert, 1783) and *Ardea cocoi* Linnaeus, 1766, did not vary among the four phases of the seasonal cycle. *Ixobrychus exilis* and *P. pileatus*, on the other hand, were recorded only in the phase with waters at lowest level and *C. cochlearius* was recorded in both this and rising phases. (Table 2).

Table 2. Species abundance registered during each phase of the seasonal cycle (see the text for details of the characteristics of each phase). The last row shows the p values of the χ^2 test, comparing the abundance of each species among the phases of the seasonal cycle. The taxonomy follows CBRO (2015).

| Species | Phases | | | | p |
|---|--------|------|--------|------------|--------|
| | Ebb | Dry | Rising | Peak-flood | |
| <i>Tigrisoma lineatum</i> (Boddaert, 1783) | 32 | 49 | 40 | 40 | 0.3100 |
| <i>Cochlearius cochlearius</i> (Linnaeus, 1766) | 0 | 9 | 2 | 0 | – |
| <i>Ixobrychus exilis</i> (Gmelin, 1789) | 0 | 1 | 0 | 0 | – |
| <i>Nycticorax nycticorax</i> (Linnaeus, 1758) | 4 | 23 | 16 | 7 | 0.0040 |
| <i>Butorides striata</i> (Linnaeus, 1758) | 67 | 91 | 6 | 17 | 0.0001 |
| <i>Bubulcus ibis</i> (Linnaeus, 1758) | 135 | 192 | 114 | 361 | 0.0001 |
| <i>Ardea cocoi</i> Linnaeus, 1766 | 18 | 30 | 26 | 17 | 0.1500 |
| <i>Ardea alba</i> Linnaeus, 1758 | 80 | 817 | 259 | 137 | 0.0001 |
| <i>Pilherodius pileatus</i> (Boddaert, 1783) | 0 | 1 | 0 | 0 | – |
| <i>Egretta thula</i> (Molina, 1782) | 64 | 363 | 179 | 32 | 0.0001 |
| <i>Egretta caerulea</i> (Linnaeus, 1758) | 4 | 41 | 1 | 14 | 0.0001 |
| Total | 404 | 1617 | 643 | 625 | 0.0001 |

In the use of the microhabitat, in the phase that the water level was lowering, axes 1 and 2 of the CA ordination account for 64% and 19% of the data variation, respectively. In this phase, we found that the abundance of *T. lineatum* (100%), *A. cocoi* (80%), *E. thula* (73%), *A. alba* (69%), *B. striata* (67%) and *B. ibis* (64%) was influenced by aquatic macrophytes (Fig. 2, Table 3).

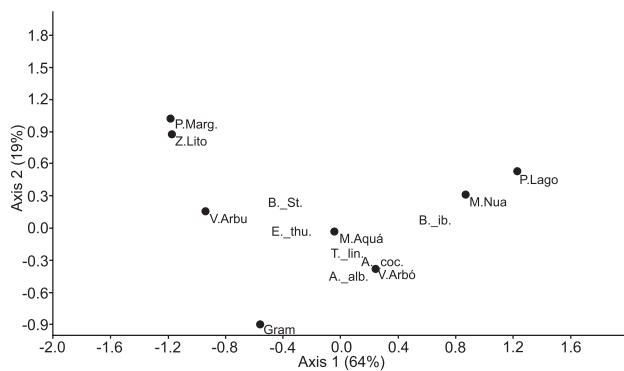


Figure 2. Correspondence analysis of the species of the family Ardeidae with the microhabitats explored by them during the ebb phase (descent of water level) in floodplain lakes of the low Amazon River. Acronyms for species' names and microhabitats are presented in Table 3.

In the phase with lowest water levels, the ordination of the CA data on axes 1 and 2 was responsible for 64% and 36% of the variation, respectively. The results of the CA suggest that the occurrence of *T. lineatum* (76%), *B. striata* (68%), *N. nycticorax* (57%), *E. thula* (45%) and *A. cocoi* (40%) might have been influenced by aquatic macrophytes. Records of *A. alba* were also associated with this microhabitat (37%) and with arboreal vegetation (26%). The occurrence of *E. caerulea* (66%)

was strongly influenced by the presence of shrubs, whereas *B. ibis* occurred in association with bare margin (28%) and grass (27% Fig. 3, Table 3).

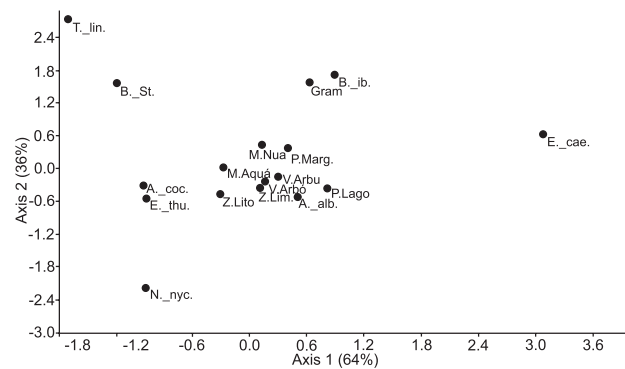


Figure 3. Correspondence analysis of the species of the family Ardeidae with the microhabitats explored by them during the dry phase (waters at lowest level) in floodplain lakes of the low Amazon River. Acronyms for species names and microhabitats are presented in Table 3.

In the water level rise phase, ordination of the CA data on axes 1 and 2 represented 90% and 6% of the data variation, respectively. In this phase *E. thula* (71%), *A. cocoi* (69%), *T. lineatum* (68%), *A. alba* (64%), and *B. striata* (50%) have been influenced by aquatic macrophytes. *Bubulcus ibis* (88%) was influenced by perch margin and *N. nycticorax* (81%) was associated with arboreal vegetation (Fig. 4, Table 3).

In the peak-flood phase, ordination of the CA data on axes 1 and 2 was responsible for 65% and 26% of the data variation, respectively. In this phase, the occurrence of *A. cocoi* (94%), *B. ibis* (84%), *A. alba* (73%), *T. lineatum* (72,5%), and *E. thula* (69%)

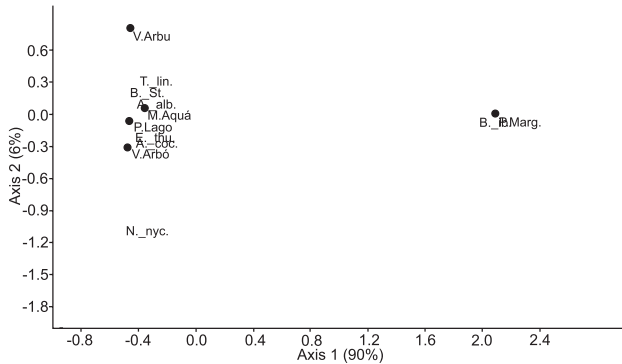


Figure 4. Correspondence analysis of the species of the family Ardeidae with the microhabitats explored by them during the rising phase (elevation of water level) in floodplain lakes of the low Amazon River. Acronyms for species names and microhabitats are presented in Table 3.

have been influenced by aquatic macrophytes. *Egretta caerulea* and *B. striata* were influenced by aquatic macrophytes (57%, 53%) and arboreal vegetation (43%, 42%), respectively. *Nycticorax nycticorax* occurred in association with two microhabitats at this stage, arboreal vegetation and shrubby vegetation (57% and 43%), respectively (Fig. 5, Table 3).

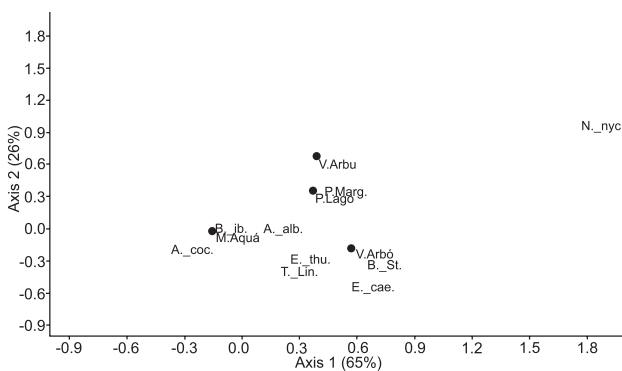


Figure 5. Correspondence analysis of the species of the family Ardeidae with the microhabitats explored by them during the peak-flood phase (sustained water level acme) in floodplain lakes of the low Amazon River. Acronyms for species names and microhabitats are presented in Table 3.

DISCUSSION

In our data, the abundance of most Ardeidae recorded varied throughout the seasonal cycle of the Amazon floodplains. Ardeid birds also seemed to have a preference for the aquatic macrophytes microhabitat (Hancock and Kushlan 1984, Gimenes and Anjos 2006, Pimenta et al. 2007, Kushlan, 2011). Some species were more abundant at a given phase and others

were recorded at only some phases of the seasonal cycle, which suggests that the entire population or part of the population of some species move away at some phase of the seasonal cycle. However, it is important to point out that even though moving away is a plausible hypothesis for the observed variations in the numbers of individuals recorded at each phase, this hypothesis needs further testing. Other studies also had shown that part of the populations of some Ardeidae species migrate our move seasonally (Olmos and Silva 2001, Antas and Palo-Júnior 2004, Nunes and Tomas 2008). This displacement may be correlated with two factors: 1) the presence (or absence) of resources (i.e. food); 2) the degree of specialization of the species. The microhabitat explored by some, but not all, ardeid birds, varied throughout the year.

Among the six species that varied in abundance between the four phases of the seasonal cycle, five were more abundant during the dry season, with waters at lowest level. In this phase, there is frequently an increase in the abundance of waterbirds in lakes located in areas that get periodically flooded (e.g., Guadagnin et al. 2005, Accordi and Hartz 2006, Soares and Rodrigues 2009, Gimenes and Anjos 2011, Cintra 2012, Tavares and Siciliano 2014). The most common justification for this pattern is that food resources become very concentrated in these lakes during the dry period, which the waterbirds come to exploit (Gimenes and Anjos 2006, Cintra et al. 2007).

Bubulcus ibis was the only Ardeidae recorded in this study that was more abundant in the peak-flood phase, with waters at highest level. This species is native to Africa and Mediterranean Europe (Rice 1956) and is associated with large grazing mammals rather than with aquatic environments (Martínez-Vilalta et al. 2014a). This species was first recorded in Brazil in 1964 (Sick 1965), where its occurrence is facilitated by the presence of livestock (Sick 1997, Bella and Azevedo-Júnior 2004, Seedikkoya et al. 2005, Nunes et al. 2010, Morales-Silva and Lama 2014). It is commonly found foraging among cattle (Gasset et al. 2000, Martínez-Vilalta et al. 2014a) and capturing the insects that are associated with or get displaced by these large animals. In the study region, during the peak-flood phase, herds are transferred from the floodplain to slightly higher and non-flooded regions, and during this time *B. ibis* individuals concentrate at the marginal vegetation of the lakes. However, our results do not clarify why these birds did not accompany the cattle herds when they were transferred to drier areas, or even whether some birds did follow the cattle there.

In general, in the present study, the microhabitat preferred by most species of Ardeidae throughout the year was aquatic macrophytes. This preference is possibly related to the diet of these birds (Gimenes and Anjos 2006, Alves et al. 2012). Aquatic organisms, such as fish and invertebrates, on which the Ardeidae feed, use macrophytes for shelter and reproduction (Oliveira and Goulart 2000). Another possibility, suggested by Gimenes and Anjos (2011), is that this microhabitat allows some species, especially the smaller ones, to use areas located further away from

Table 3. Percentage relation of correspondence analysis among species and microhabitats during each phase of the season cycle. Between parentheses, the species and the microhabitats presented in the CCA of each phase.

| Phases | Species | Aquatic macrophyte | Arboreal vegetation | Shrub vegetation | Grass | Naked margin | Lake perch | Lake margin | Limnetic zone | Coastal zone |
|------------|------------------------------|--------------------|---------------------|------------------|-------|--------------|------------|-------------|---------------|--------------|
| Ebb | <i>Tigrisoma lineatum</i> | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | <i>Nycticorax nycticorax</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | <i>Butorides striata</i> | 67 | 6 | 15 | 0 | 3 | 0 | 6 | 0 | 3 |
| | <i>Bubulcus ibis</i> | 64 | 8 | 0 | 0 | 27 | 1 | 0 | 0 | 0 |
| | <i>Ardea cocoi</i> | 80 | 13 | 0 | 0 | 7 | 0 | 0 | 0 | 0 |
| | <i>Ardea alba</i> | 69 | 15 | 8 | 4 | 5 | 0 | 0 | 0 | 0 |
| | <i>Egretta thula</i> | 73 | 0 | 17 | 3 | 3 | 0 | 2 | 0 | 2 |
| | <i>Egretta caerulea</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Dry | <i>Tigrisoma lineatum</i> | 76 | 8 | 8 | 2 | 4 | 0 | 2 | 0 | 0 |
| | <i>Nycticorax nycticorax</i> | 57 | 35 | 9 | 0 | 0 | 0 | 0 | 0 | 0 |
| | <i>Butorides striata</i> | 68 | 14 | 9 | 2 | 2 | 0 | 2 | 2 | 0 |
| | <i>Bubulcus ibis</i> | 20 | 11 | 9 | 27 | 28 | 0 | 6 | 0 | 0 |
| | <i>Ardea cocoi</i> | 40 | 17 | 3 | 0 | 13 | 0 | 3 | 3 | 20 |
| | <i>Ardea alba</i> | 37 | 26 | 20 | 0 | 5 | 2 | 3 | 3 | 8 |
| | <i>Egretta thula</i> | 45 | 9 | 18 | 1 | 11 | 0 | 0 | 2 | 13 |
| | <i>Egretta caerulea</i> | 12 | 2 | 66 | 0 | 7 | 5 | 0 | 2 | 5 |
| Rising | <i>Tigrisoma lineatum</i> | 68 | 20 | 13 | 0 | 0 | 0 | 0 | 0 | 0 |
| | <i>Nycticorax nycticorax</i> | 19 | 81 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | <i>Butorides striata</i> | 50 | 33 | 17 | 0 | 0 | 0 | 0 | 0 | 0 |
| | <i>Bubulcus ibis</i> | 12 | 0 | 0 | 0 | 0 | 0 | 88 | 0 | 0 |
| | <i>Ardea cocoi</i> | 69 | 31 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | <i>Ardea alba</i> | 64 | 26 | 9 | 0 | 0 | 0 | 1 | 0 | 0 |
| | <i>Egretta thula</i> | 71 | 28 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| | <i>Egretta caerulea</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Peak-flood | <i>Tigrisoma lineatum</i> | 73 | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | <i>Nycticorax nycticorax</i> | 0 | 57 | 43 | 0 | 0 | 0 | 0 | 0 | 0 |
| | <i>Butorides striata</i> | 53 | 42 | 5 | 0 | 0 | 0 | 0 | 0 | 0 |
| | <i>Bubulcus ibis</i> | 84 | 10 | 6 | 0 | 0 | 0 | 0 | 0 | 0 |
| | <i>Ardea cocoi</i> | 94 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | <i>Ardea alba</i> | 73 | 18 | 7 | 0 | 0 | 1 | 1 | 0 | 0 |
| | <i>Egretta thula</i> | 69 | 28 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| | <i>Egretta caerulea</i> | 57 | 43 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

the shore, allowing greater exploration of the area, regardless of the depth of the lake. Those authors observed this behavior in *B. striata* at the Paraná River.

According to Gimenes and Anjos (2011), *A. cocoi*, *A. alba* and *T. lineatum* did not demonstrate a clear preference for a particular habitat of the Paraná River, whereas Pinto et al. (2013) reported that *A. cocoi* and *A. alba* used similar substrates in the presence or absence of water. This results differ from ours, since in our data these species showed preference for aquatic macrophytes in the four phases of the seasonal cycle. These species have a wide geographical distribution and it is possible that their supply of resources and habitats vary throughout their distribution range. We suggest that these Ardeid birds are generalists, but generally prefer to use macrophytes when such plants are available. We are aware of one exception to this, in

the results of Pimenta et al. (2007), who demonstrated that *E. thula* does not occur in association with aquatic macrophytes at the *Pampulha* Lake, even though these plants were abundant at the site. This difference in habitat use is not surprising since these species have a wide geographic distribution and possibly the supply of resources and habitats should change throughout their distributions.

Relatively few Ardeidae species used microhabitats other than macrophytes. *Nycticorax nycticorax* was recorded more often in arboreal vegetation and shrub vegetation in two phases. This species exhibits crepuscular and nocturnal habits (Martínez-Vilalta et al. 2014b), as well as *Cochlearius cochlearius*. It is possible that the microhabitat where *N. nycticorax* was more often recorded in this study corresponds to its resting habitat, and that it uses other microhabitats to forage in the twilight

and nocturnal periods. *Egretta caerulea* showed a preference for shrub vegetation in the phase with waters at lowest level, and for tree vegetation in the peak-flood phase. According to Martínez-Vilalta et al. (2014c), *E. caerulea* is partly insectivorous, being able to look for insects in vegetation distant from the water. In addition, Sick (1997) mentioned that this species also feeds on the insects that are scared by cattle. This is also the case of *B. ibis*. This may be the reason why we recorded it, in this study, on shrub vegetation and arboreal vegetation.

In two phases of the cycle, the occurrence of *B. ibis* was more strongly correlated with microhabitats other than aquatic macrophytes: bare and grassy margin in the phase with waters at lowest level and perch margin in the rising phase. As mentioned above, this species displays an opportunistic feeding behavior (Gasset et al. 2000), foraging among bovine cattle. Pinto et al. (2013) observed that this species has a preference for dry microhabitats, which is possibly related to its association with large grazing mammals. In the present study, this species used macrophytes and perch margin only when the microhabitats such as bare margin and grasses were submerged.

The preference of the Ardeid birds for aquatic macrophytes throughout the seasonal cycle suggests that this may be a key microhabitat for the maintenance of this family (and probably of its preys) in Amazonian floodplains. This preference may be related to the diet of these birds, or to a greater exploitation of the environment during the different phases of the seasonal cycle. In addition, the occurrence of rare species (eg. *I. exilis* and *P. pileatus*) and the strong preference of ardeid species for specific microhabitats demonstrate the importance of preserving this region. It is important to emphasize that the floodplains are one of the most fragile Amazon ecosystems and are amongst the most affected by anthropic activities, which makes them even more relevant to conservation.

ACKNOWLEDGMENTS

We thank Universidade Federal do Oeste do Pará and Programa de Pós-Graduação em Recursos Aquáticos Continentais for the structure and logistic support; Coodenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the fellowship granted to the first and second authors (prossces 1224657 and 1231796, respectively); the residents of the community of Santa Maria do Taparará, especially Lauro Almeida and Rosenira Almeida, for logistical support during field work.

LITERATURE CITED

- Accordi IA, Hartz SM (2006) Distribuição espacial e sazonal da avifauna em uma área úmida costeira do sul do Brasil. *Revista Brasileira de Ornitologia* 14(2): 117–135.
- Accordi IA (2010) Pesquisa e conservação de aves em áreas úmidas. In: Matter SV, Straube FC, Accordi IA, Piacentini V, Cândido-JR JF (Eds) *Ornitologia e Conservação: ciência aplicada, técnicas de pesquisa e levantamento*. Rio de Janeiro, Technical Books, 191–216.
- Alves MAS, Lagos AR, Vecchi MB (2012) Uso do habitat e táticas de forrageamento de aves aquáticas na Lagoa Rodrigo de Freitas, Rio de Janeiro, Brasil. *Oecologia Australis* 16(3): 525–539. <https://doi.org/10.4257/oeco.2012.1603.12>
- Antas PTZ (1994) Migration and other movements among the lower Paraná River valley wetlands, Argentina, and the south Brazil/Pantanal wetlands. *Bird Conservation International* 4: 181–190.
- Antas PTZ, Palo-Júnior H (2004) Guia de aves: espécies da reserva particular do patrimônio natural do SESC Pantanal. Rio de Janeiro, SESC Nacional, 249 pp.
- Bancroft TG, Gawlick DE, Rutchey K (2002) Distribution of wading birds relative to vegetation and water depths in the northern Everglades of Florida, USA. *Waterbirds* 25: 265–277. [https://doi.org/10.1675/1524-4695\(2002\)025\[0265:DOWBRT\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2002)025[0265:DOWBRT]2.0.CO;2)
- Bella SD, Azevedo-Júnior SM (2004). Considerações sobre a ocorrência da Garça-vaqueira, *Bubulcus ibis* (Linnaeus) (Aves, Ardeidae) em Pernambuco, Brasil. *Revista Brasileira de Zoologia* 21(1): 57–63. <https://doi.org/10.1590/S0101-81752004000100011>
- Bibby CJ, Burguess NDE, Hill DA (1992) *Bird census techniques*. London, Academic Press, 257 pp.
- Cintra R (2012) Ecological Gradients Influencing Waterbird Communities in BlackWater Lakes in the Anavilhanas Archipelago, Central Amazonia. *International Journal of Ecology* 2012: e801683. <https://doi.org/10.1155/2012/801683>
- Cintra R, Santos PMRS, Leite CB (2007) Composition and structure of the lacustrine bird communities of seasonally flooded wetlands of western Brazilian Amazonia at high water. *Waterbirds* 30: 521–540.
- Dimalexis A, Pyrovetsi M, Sgardelis S (1997) Foraging ecology of the Grey Heron (*Ardea cinerea*), Great Egret (*Ardea alba*) and Little Egret (*Egretta garzetta*) in response to habitat, at 2 Greek wetlands. *Colonial Waterbirds* 20: 261–272.
- Figueira JEC, Cintra R, Viana LR, Yamashita C (2006) Spatial and temporal patterns of bird species diversity in the Pantanal of Mato Grosso, Brazil: implications for conservation. *Brazilian Journal of Biology* 66(2A): 393–404. <https://doi.org/10.1590/S1519-69842006000300003>
- Fine VAP (2015) Ecological and evolutionary drivers of geographic variation in species diversity. *Annual Review of Ecology, Evolution, and Systematics* 46: 369–392. <https://doi.org/10.1146/annurev-ecolsys-112414-054102>
- Fowler J, Cohen L (1995) *Statistics for ornithologists*. Norwich, British Trust for Ornithology, Guide 22, 2nd ed., 176 pp.
- Fraxe TJP, Pereira HS, Witkoski AC (2007) Comunidades Ribeirinhas Amazônicas: modos de vida e uso dos recursos naturais. Manaus, Universidade Federal do Amazonas, Projeto Piatam, 223 pp.
- Gasset JW, Folk TH, Alexy KJ, Miller KV, Chapman BR, Boyd FL, Hall DI (2000) Food habits of Cattle Egrets on St. Croix, U.S. Virgin Islands. *Wilson Bulletin* 112(2): 268–271.

- Gimenes MR, Anjos L (2006) Influence of Lagoons Size and Prey Availability on the Wading Birds (Ciconiiformes) in the Upper Paraná River Floodplain, Brazil. *Brazilian Archives of Biology and Technology* 49(3): 463–473. <https://doi.org/10.1590/S1516-89132006000400015>
- Gimenes MR, Anjos L (2011) Quantitative Analysis of Foraging Habitat Use by Ciconiiformes in the Upper Paraná River Floodplain, Brazil. *Brazilian Archives of Biology and Technology* 54 (2): 415–427. <https://doi.org/10.1590/S1516-89132011000200025>
- Gonçalves MT, Santos RS (2009) Aplicação da Análise de Correspondência à Avaliação Institucional da Fecilcam. *Revista Nupam* 1(1): 1–14.
- Guadagnin DL, Peter AS, Perello LFC, Maltchik L (2005) Spatial and temporal patterns of waterbird assemblages in fragmented wetlands of southern Brazil. *Waterbirds* 28(3): 261–272.
- Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4: 1–9. Available online at: http://palaeo-electronica.org/2001_1/past/issue1_01.htm [Accessed: 23/07/2014]
- Hancock J, Elliott H (1978) *The herons of the world*. London, Editions, 304 pp.
- Hancock J, Kushlan JA (1984) *The herons handbook*. London, Croom Helm, 288 pp.
- Huchtnson GE (1957) Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22: 415–427.
- Inmet (2013) Instituto Nacional de Meteorologia. Available online at: <http://www.inmet.gov.br> [Accessed: 23/06/2013]
- Isacch JP, Martínez MM (2003) Habitat use by nonbreeding shorebirds in flooding pampas grasslands of Argentina. *Waterbirds* 26: 494–500. [https://doi.org/10.1675/1524-4695\(2003\)026\[0494:HUBNSI\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2003)026[0494:HUBNSI]2.0.CO;2)
- Junk WJ, Bayley PB, Sparks RE (1989) The Flood Pulse Concept in River-Floodplain Systems. In: Dodge DP (Ed.) *Proceedings of the International Large River Symposium*. Campaign, Canadian Special Publication of Fisheries and Aquatic Sciences, 110–127.
- Kushlan JA (2011) *The Terminology of Courtship, Nesting, Feeding and Maintenance in Herons*. Heron Conservation. Available online at: <http://www.heronconservation.org> [Accessed: 08/01/2019]
- Legendre P, Legendre L (1998) *Numerical Ecology*. Amsterdam, Elsevier Science, 852 pp.
- Lopes EV, Volpato GH, Mendonça LB, Fávaro FL, Anjos L (2006) Abundância, microhabitat e repartição ecológica de papa-formigas (Passeriformes, Thamnophilidae) na bacia hidrográfica do rio Tibagi, Paraná, Brasil. *Revista Brasileira de Zoologia* 23(2): 395–403. <https://doi.org/10.1590/S0101-81752006000200013>
- Martínez-Vilalta A, Motis A, Kirwan GM (2014a) Cattle Egret (*Bubulcus ibis*). In: Del Hoyo J, Elliott A, Sargatal J, Christie DA, De Juana E (Eds) *Handbook of the Birds of the World Alive*. Barcelona, Lynx Edicions. Available online at: <http://www.hbw.com/node/52697> [Accessed: 14/05/2015]
- Martínez-Vilalta A, Motis A, Kirwan GM (2014b) Black-crowned Night-heron (*Cochlearius cochlearius*). In: Del Hoyo J, Elliott A, Sargatal J, Christie DA, De Juana E (Eds) *Handbook of the Birds of the World Alive*. Barcelona, Lynx Edicions. Available online at: <http://www.hbw.com/node/5270>. [Accessed: 14/05/2015]
- Martínez-Vilalta A, Motis A, Kirwan GM (2014c) Little Blue Heron (*Egretta caerulea*). In: Del Hoyo J, Elliott A, Sargatal J, Christie DA, De Juana E (Eds) *Handbook of the Birds of the World Alive*. Barcelona, Lynx Edicions. Available online at: <http://www.hbw.com/node/52692>. [Accessed: 14/05/2015]
- Morales-Silva E, Lama SND (2014) Colonization of Brazil by the cattle egret (*Bubulcus ibis*) revealed by mitochondrial DNA. *NeoBiota* 21: 49–63. <https://doi.org/10.3897/neobiota.21.4966>
- Nunes AP, Tomas WM (2008) Aves migratórias e nômades ocorrentes no Pantanal. Corumbá, Embrapa Pantanal, 124 pp.
- Nunes MFC, Barbosa-Filho RC, Roos AL, Mestre LAM (2010) The Cattle Egret (*Bubulcus ibis*) on Fernando de Noronha Archipelago: history and population trends. *Revista Brasileira de Ornitologia* 18(4): 315–327.
- Oliveira EF, Goulart E (2000) Distribuição espacial de peixes em ambientes lênticos: interação de fatores. *Acta Scientiarum* 22(2): 445–453.
- Olmos F & Silva R (2001) The avifauna of a southeastern Brazilian mangrove swamp. *International Journal of Ornithology* 4 (3/4): 135–205.
- Petermann P (1997) *The birds*. In: Junk WJ (Ed.) *The Central Amazon Floodplain: Ecology of a Pulsing System*. Heidelberg, Springer-Verlag, Berlin, 419–451.
- Piedade MTF (1995) Influência do Pulso de Cheias e Vazantes na Dinâmica Ecológica de Áreas Inundáveis. Projeto de Pesquisa Dirigida. Brasília, INPA, 446 pp.
- Pimenta FE, Drummond JCP, Lima AC (2007) Aves aquáticas da Lagoa da Pampulha: seleção de habitats e atividade diurna. *Lundiana* 8(2): 89–96.
- Pinto DP, Chivittz CC, Tozetti AM (2013) Microhabitat use by three species of egret (Pelecaniformes, Ardeidae) in southern Brazil. *Brazilian Journal of biology* 73(4): 791–796.
- Ribeiro NV (2007) *Atlas da várzea: Amazônia Brasil*. Manaus, Ibama, 132 pp.
- Rice DW (1956) Dynamics of range expansion of Cattle Egrets in Florida. *The Auk* 73(2): 259–266.
- Rohde K (1992) Latitudinal Gradients in Species Diversity: The Search for the Primary Cause. *Oikos* 65(3): 514–527.
- Seedikkoya K, Azeez PA, Shukkur AA (2005) Cattle Egret *Bubulcus ibis* habitat use and association with cattle. *Forktail* 21: 174–175.
- Sick H (1965) *Bubulcus ibis* (Linnaeus) na Ilha de Marajó, Pará: Garça ainda não registrada no Brasil. *Anais da Academia*

- Brasileira de Ciências 37: 567–570. <https://doi.org/10.1590/S0101-81752004000100011>
- Sick H (1997) Ornitologia brasileira. Rio de Janeiro, Nova Fronteira, 862 pp.
- Silva JMC, Bates JM (2002) Biogeographic patterns and conservation in the South American Cerrado: a Tropical Savanna Hotspot. *BioScience* 52: 225–233.
- Sioli H (1985) Amazônia: Fundamentos da ecologia da maior região de florestas tropicais. Petrópolis, Editora Vozes, 69 pp.
- Soares RKP, Rodrigues AAF (2009) Distribuição espacial e temporal da avifauna aquática no Lago de Santo Amaro, Parque Nacional dos Lençóis Maranhenses, Maranhão, Brasil. *Revista Brasileira de Ornitologia* 17(3–4): 173–182.
- Statsoft (2004) Statistica. Statsoft Inc, v. 7.0. Available online at: <http://www.statsoft.com>
- Stotz DF, Fitzpatrick JW, Parker III TA, Moskovits DK (1996) Neotropical Birds: Ecology and Conservation. Chicago, The University of Chicago Press, 478 pp.
- Tavares DC, Siciliano S (2014) Variação temporal na abundância de espécies de aves aquáticas em uma lagoa costeira do Norte Fluminense, sudeste do Brasil. *Biotemas* 27: 121–132.
- Thompson R, Townsend C (2006) A truce with neutral theory: local deterministic factors, special traits and dispersal limitations determine patterns of diversity in streams invertebrates. *Journal of Animal Ecology* 75: 464–474.
- Willig MR, Presley SJ (2018) Latitudinal Gradients of Biodiversity: Theory and Empirical Patterns. *Encyclopedia of the Anthropocene* 3: 13–19. <https://doi.org/10.1016/B978-0-12-809665-9.09809-8>
-
- Submitted: October 10, 2018
Accepted: February 20, 2019
Available online: July 31, 2019
Editorial responsibility: Luís Fábio Silveira
-
- Author Contributions: GSF and DAAS had collected data in field work and the three authors had contributed equally to the construction of this article.
Competing Interests: The authors have declared that no competing interests exist.
© 2019 Sociedade Brasileira de Zoologia. Published by Pensoft Publishers at <https://zoologia.pensoft.net>