Reports on the ecology and behavior of Ardeidae (herons and egrets) and Threskiornithidae (Scarlet Ibis) species of a reproductive colony in a tropical estuary, São Paulo, Brazil

Relatos sobre a ecologia e o comportamento de espécies de Ardeidae (garças e socós) e Threskiornithidae (guará) em uma colônia reprodutiva em um estuário tropical no estado de São Paulo, Brasil

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Abstract: Birds from the families Ardeidae and Threskiornithidae commonly group together into intraspecific and heterospecific aggregations. In Brazil, most studies have focused on ecological and behavioral aspects related to foraging with comparatively few investigations addressing reproductive activities. This study describes a reproductive colony of these two families located in *Parque Estadual Ilha do Cardoso* on the southern coast of the State of São Paulo, Brazil. We focused on spatial use and behavioral interactions during the breeding season, and recorded six species nesting at the site. Clear differences among species were observed over three breeding seasons, including variations in reproductive period length and colony occupation patterns. Additionally, we recorded behavioral interactions such as agonistic behaviors and biparental care in the Scarlet Ibis. Notable differences in nestling and chick behavior were observed, particularly regarding nest agitation and their ability to move through vegetation. Importantly, the initial dynamic of colony occupation was marked by the arrival of a large number of Scarlet Ibis individuals. These findings underscore the importance of long-term studies to better understand the ecological relationships underlying the breeding dynamics of colonial waterbirds.

Keywords: *Ardea alba*. *Egretta thula*. *Egretta caerulea*. *Nycticorax nycticorax*. *Nyctanassa violacea*. *Eudocimus ruber*.

Resumo: Aves das famílias Ardeidae e Threskiornithidae geralmente se agrupam em agregações intraespecíficas e heteroespecíficas. No Brasil, a maioria dos estudos aborda as relações ecológicas e comportamentais apenas durante as atividades de forrageamento, e não durante as atividades reprodutivas. Diante disso, o presente estudo teve como objetivo descrever uma colônia reprodutiva dessas duas famílias (famílias Ardeidae e Threskiornithidae) localizada no Parque Estadual Ilha do Cardoso, no litoral sul do estado de São Paulo, Brasil, e descrever a organização espacial e temporal da colônia, bem como as interações comportamentais entre as espécies. Foram registradas seis espécies utilizando o local para reprodução, com variações anuais na ocupação da colônia e na duração do período reprodutivo. Também foram observadas interações comportamentais, como agonismo e o cuidado biparental entre os guarás (*Eudocimus ruber*). Entre os ninhegos, destacaram-se as diferenças comportamentais quanto à inquietação no ninho e à agilidade no deslocamento pela vegetação. Por fim, enfatizamos que a ocupação espacial e a dinâmica reprodutiva da colônia são influenciadas diretamente pela chegada dos guarás. Além disso, ressaltamos a importância de estudos de longa duração para a compreensão das relações ecológicas que fundamentam a dinâmica de reprodução destas espécies.

Palavras-chave: *Ardea alba*. *Egretta thula*. *Egretta caerulea*. *Nycticorax nycticorax*. *Nyctanassa violacea*. *Eudocimus ruber*.

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INTRODUCTION

Most species in the families Ardeidae (egrets and herons) and Threskiornithidae (ibises and spoonbills) are closely associated with aquatic environments. Many of these species use coastal ecosystem and mangroves as key areas for foraging and breeding (Custer et al., 1980; Sick, 2001). They are among the main predators of fishes and marine invertebrates in estuarine environments (Frederick, 2002; Faria et al., 2016; Dias et al., 2025).

Intraspecific and interspecific aggregations of Ardeidae and Threskionithidae are commonly observed during foraging, resting, migration, and nesting events (Kushlan & Hancock, 2005). These aggregations offer individuals protection and allow for optimal resource exploitation (Burger, 1981; Huang et al., 2021).

For most species, a key reproductive trait is their tendency to form monospecific or mixed-species colonies, with the number of species varying according to location (Kushlan & Hancock, 2005). Although the reproductive period may shift annually due to climate factors and food availability (Nachuha & Ejotre, 2014; Baker & Dieter, 2015), in Brazil these events typically begin in the austral spring (September to December) and may extend in to the austral autumn (March to June; Sick, 2001).

Colony site selection is influenced by the proximity to feeding areas, the presence of vegetation that offers nest protection, accessibility, and the characteristics of the surrounding habitat (McCrimmon Jr., 1978; van Vessem & Draulans, 1987; Frederick, 2002; Carrasco et al., 2014, 2017). Nest structures vary among species and are typically built in trees, bushes, thicket over water, and mangroves (Angehr & Kushlan, 2007; Ayala, 2022). Major limiting factors for reproductive success include nest abandonment by adults, chicks falling from nests, predation, and adverse weather condition (Frederick & Collopy, 1989; Hafner et al., 2008).

Vertical stratification of nets within colonies has been observed, generally occupying higher canopy levels and smaller species nesting in lower vegetation or understory (Burger & Gochfeld, 1990; Ayala, 2022). Furthermore, more experienced individuals tend to nest in the interior of the colony, while less experienced birds are more often found at the edges (Burger, 1981).

Although birds from the Ardeidae and Threskiornithidae families are considered relatively well-studied group, understanding their reproductive ecology remains important. Information on their breeding dynamics is essential for developing effective conservation strategies (Kushlan, 2018). Moreover, in Brazil most behavioral studies on these families have focused on foraging ecology, with relatively few addressing behavior and ecological dynamics during the reproductive period – particularly within heterospecific colonies, with emphasis on De Toledo (2000), Scherer et al. (2014), Paludo et al. (2018), Martínez et al. (2020) and Cabral et al. (2023). In this study, we describe the ecology and behavior of Ardeidae (herons and egrets) and Threskiornithidae (Scarlet Ibis) species within a reproductive colony in a tropical estuary in Brazil, monitored over three breeding seasons.

MATERIAL AND METHODS

STUDY AREA

This study was conducted in *Parque Estadual Ilha do Cardoso*, a state park that protects remnants of the Atlantic Forest biome (25° 07' 29" S and from 47° 57' 44" W; 0 m to 800 m altitudinal variation). The park is located on Cardoso Island, along the southern coast of the State of São Paulo, Brazil (Figure 1). The climate is classified as hot and humid, with average temperature ranging from 19 °C to 27 °C, and a mean annual precipitation of 2,802 mm (based on data from 2019) (CIIAGRO, 2020).

NEST CHARACTERIZATION

The bird colonies were located at the southern end of the island (25° 17' 58" S; 48° 05' 29.6" W; altitude ranging

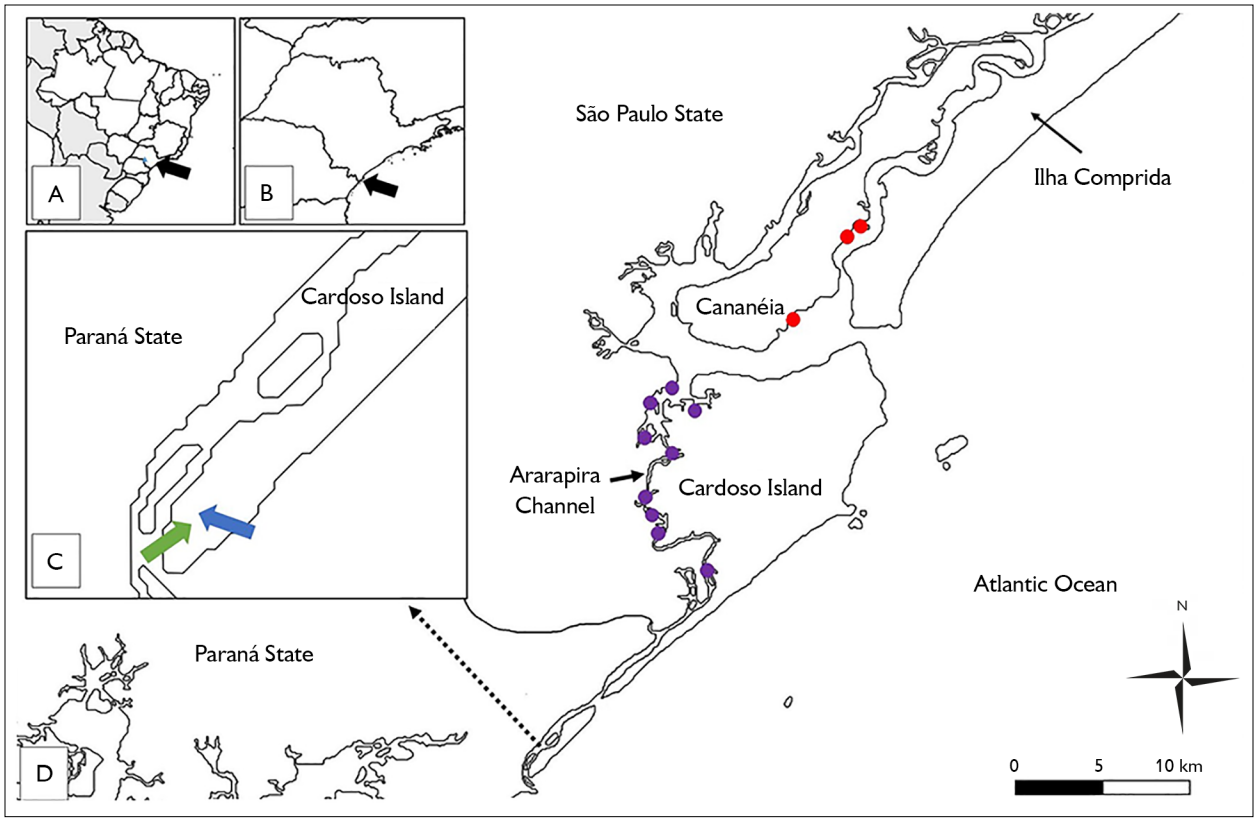

Figure 1. Geographic location of Cardoso Island on the southern coast of São Paulo State (A, B), Brazil. (C) Green arrow indicates the nesting colony area; blue arrow marks the Pontal do Leste Community. Red points represent foraging areas in Cananéia, while purple points indicate foraging areas along the Ararapira Channel (D). Map: Henrique Chupil (2025).

from 0 m to 5 m), near the Pontal do Leste Community. The site is bordered to the west by the Ararapira Channel and to the east by the Atlantic Ocean (Figure 1). The area encompasses approximately 20,000 m^2. Water volume changes according to the tides (Figure 2), with tidal inflow entering the lagoon through a stream connected to the Ararapira Channel.

The lagoon is surrounded by three mangrove species: *Avicenia schaueriana* Stapf & Leechm. ex Moldenke, *Rizophora mangle* L., and *Laguncularia racemosa* (L.) C.F. Gaertn. (Figure 2B). A sand strip separates the lagoon from the Atlantic Ocean, which is vegetated by *Hibiscus pernambucensis* Arruda, *Psidium cattleyanum* Afzel. ex Sabine, *Conocarpus erectus* L., and other shrub species, along with marsh areas dominated by *Typha latifolia* L. (Cunha-Lignon et al., 2011). The distance between the beach and the lagoon varies from 50 to 70 meters.

The identification of the reproductive species present in the colonies was conducted during the first field expedition.

DATA SAMPLING

Fieldwork was conducted by one to four researches who traveled by the boat from the city of Cananéia between September and May during the 2015/2016, 2016/2017 and 2017/2018 breeding seasons, with monthly expeditions (averaging one day per month). Behavioral observations were carried out from a sand strip located to the south of the lagoon, which surrounds the nesting area. We employed naturalistic observation using scan

sampling (Altmann, 1974) to minimize disturbance to bird behavior, aided by binoculars (Bushnell 10x42). To study individual behavior and social interactions, both focal animal sampling and sequential sampling methods were used, allowing for the recording of one or more behaviors from multiple individuals. Photograph records were obtained with a Nikon camera D3300 (lens 70-300 mm) and Canon 5D Mark II (lenses 100x500 mm and 100x400 mm).

Visual assessments of bird abundance were conducted by surveying the outer perimeter of the nesting area. Egg counts were performed by approximating nest contents in accessible areas, limited to nests located up to two meters high.

To map the spatial distribution of individuals and nests within the lagoon, we conducted three short Unmanned Aerial Vehicle (UAV – DJI/Mavic) flights, each lasting 10–12 minutes, all on the same day. In addition, we periodically used a kayak to navigate within the lagoon, providing alternate visual access to the nesting area. Both UAV flights and kayak incursions maintained a minimum distance from the birds to avoid behavioral disturbance.

The identification of foraging areas beyond the Ararapira Chanel was carried out during the monthly boat

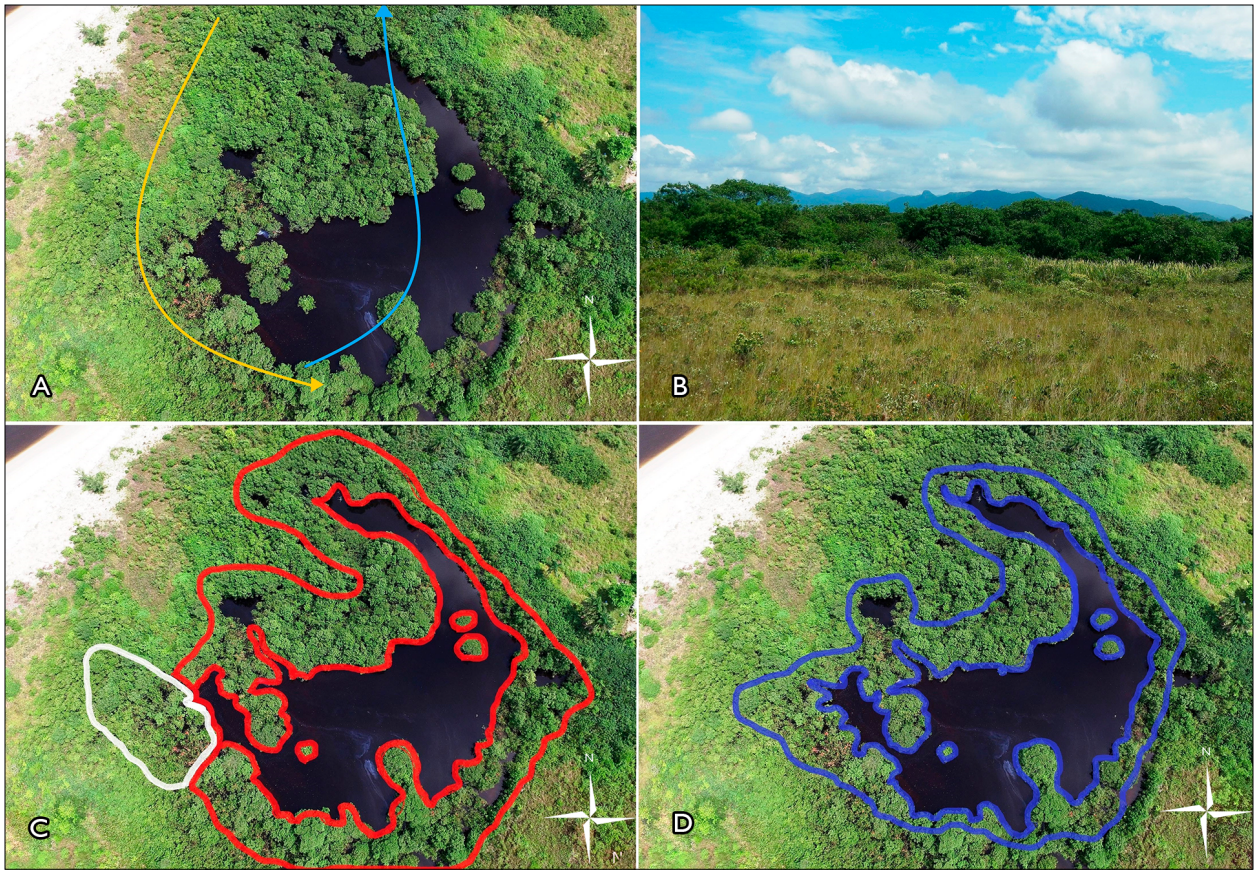

Figure 2. Nesting colony area located in the southern part of Ilha do Cardoso: A) aerial image of the lagoon: the yellow arrow indicates the flight path of birds arriving at the nesting colony, while the blue arrow indicates the path of birds departing the area; B) frontal view of the nesting colony, with shrubby vegetation in the foreground and typical mangrove species in the background surrounding the lagoon; C) distribution of the reproductive area (red polygon) and the resting/dormitory area (white polygon) during the breeding seasons from September 2015 to May 2016 and September 2017 to April 2018; D) distribution of the reproductive, dormitory, and resting areas (blue polygon) during the breeding season from September 2016 to February 2017. Images: Authors (2016).

expeditions to the reproductive colony. In Cananéia, the foraging areas were located based on monthly incursions along the center island coast. Although the birds were not banded, we inferred their use of these areas based on consistent flight, assuming that individual breeding in the colony regularly moved to these sites.

In the case of the Scarlet Ibis, it was possible to distinguish between males and females, as males typically have bills that are, on average, 22% longer than those of females and exhibit darker coloration (Hancock et al., 1992; Sick, 2001).

RESULTS

BIRD SPECIES RECORDED AND SPATIAL OCCUPATION OF NESTING AREA

We recorded six bird species breeding within the study area – five belonging to the family Ardeidae: Black-crowned Night-Heron, Yellow-crowned Night-Heron, Snowy Egret, Little Blue Heron, and Great Egret; and one species from the family Threskiornithidae: Scarlet Ibis (some examples are shown in Figure 4). Only two Great Egret nests were recorded, both observed in September 2016; located at the top of a tree on a small, isolated island within the lagoon.

The first species to arrive at the colony at the beginning of the breeding season were the Black-crowned Night-Heron and Yellow-crowned Night-Heron, followed by the Snowy Egret, Little Blue Heron, and Scarlet Ibis. Across all three reproductive seasons, Scarlet Ibis was the most abundant species in the colony (Table 1). Black-crowned Night-Heron, Yellow-crowned Night-Heron, Snowy Egret, and Great Egret were more abundant during the 2016/2017 and 2017/2018 seasons, whereas Little Blue Heron was most abundant in 2015/2016 (Table 1).

During two of the reproductive seasons, Scarlet Ibises used separate areas within the site as resting (for both breeding and non-breeding individuals) and dormitory zones (non-breeding birds only). During the incubation period, adults typically rested near their nests. Nest distribution covered a broad area of the site, while resting/dormitory areas were more spatially defined in the 2015/2016 and 2017/2018 seasons (Figure 2C). In contrast, during the 2016/2017 breeding season, nests were more concentrated in the inner portion of the lagoon, overlapping with the area previously used for resting/dormitory activities (Figure 2D). A distinct resting/dormitory area was not identified during that season. For the other species, no specific resting or dormitory zones were recorded.

Throughout the three breeding seasons, nests of Snowy Egret and Little Blue Heron were commonly located along the edge vegetation of the lagoon, especially in 2016/2017. In contrast, Black-crowned Night-Heron and Yellow-crowned Night-Heron consistently nested in elevated locations within dense vegetation farther from the lagoon, showing a stable nest placement pattern across seasons.

Table 1. Estimated average number of birds (September–May) per breeding season.

Species	Breeding Seasons		
	2015/2016	2016/2017	2017/2018
Black-crowned Night-Heron	18	70	50
Yellow-crowned Night-Heron	12	30	25
Snowy Egret	19	23	20
Little Blue Heron	30	16	15
Great Egret	1	4	2
Scarlet Ibis	1,000	400	900

Although nest construction followed a general pattern—interwoven bundles of branches—Scarlet Ibis, Black-crowned Night-Heron, and Yellow-crowned Night-Heron nests were composed of a greater number of branches. These structures appeared to be more resistant to weather, as evidenced by the low number of damaged nests observed in the subsequent breeding season.

FORAGING BEHAVIOR AND FLIGHT PATTERNS

Across all three seasons, all recorded species foraged predominantly along the Ararapira Channel, at distances ranging from 1 km (mangrove zones) to 26 km (mudflats) from the colony (Figure 1). In other seasons, birds also foraged on mudflats located on the southeastern and eastern parts of Cananéia Island, up to 40 km from the nesting site (Figure 1). Within the lagoon, foraging was recorded during low and ebb tides, when the muddy edges became exposed. These conditions allowed foraging by Little Blue Heron, juvenile Scarlet Ibises, and both species of night-herons. Other species continued to forage in shallow waters within the lagoon.

At sunrise, most adult Scarlet Ibises dispersed individually or in small groups to foraging areas to the north. At these sites, group sizes could reach up to 300 individuals (based on counts conducted in December 2018). Throughout the day, small groups (2 to 5 individuals) regularly returned to the colony to feed chicks, while others simultaneously departed for feeding grounds. By sunset, large flocks—sometimes up to 30 birds—returned to the colony to roost. During the 2015/2016 breeding season, the high density of Scarlet Ibises resulted in a shortage of suitable perching sites, leading some individuals to abandon the colony and fly westward toward the Paraná State border.

Scarlet Ibis flocks typically flew in a V-formation, a pattern commonly observed in aquatic bird species (Hummel, 1983). Most flocks approached the colony from the north via the west side, performing counterclockwise circular descents above the colony to reduce wind resistance from prevailing eastern and southern sea winds. At lower altitudes and reduced speed, individuals could safely perch on vegetation. When departing the colony, most birds first flew over the lagoon, then ascended and continued northward. This allowed us to identify distinct arrival and departure routes for the nesting area (Figure 2A).

REPRODUCTION

The longest reproductive season was recorded in 2015/2016, spanning nine months from August to May. In contrast, the 2016/2017 season lasted five months (September to February), and the 2017/2018 season extended for seven months (September to April) (Figure 3).

During the first monitored breeding season (2015/2016), nest-building began in August, and nests containing eggs were already present during the first field expedition in September. In the subsequent seasons, the earliest nest-building activity was observed in September and was initiated by the Yellow-crowned Night-Heron and Black-crowned Night-Heron. Other species began nest construction only from November onward (Figure 3). In all three seasons, egg-laying commenced immediately following nest construction.

Nestlings were observed from September to April during the 2015/2016 season, from October to February in 2016/2017, and from October to March in 2017/2018 (Figure 3). The presence of chicks was recorded from September to March in 2015/2016, and from October to February in both 2016/2017 and 2017/2018 (Figure 3). A reproductive season was considered concluded when no eggs, nestlings, or chicks were observed in the colony. These endpoints occurred in May 2016, February 2017, and April 2018, respectively.

Across all species, the number of eggs per nest ranged from one to four. The average number of nestlings per nest was two for Scarlet Ibis and three for Yellow-crowned Night-Heron, Black-crowned Night-Heron, Snowy Egret, and Little Blue Heron. Due to the dense vegetation and the limited frequency of incursions into the nesting area, it was not possible to estimate the total number of nests per species in the colony.

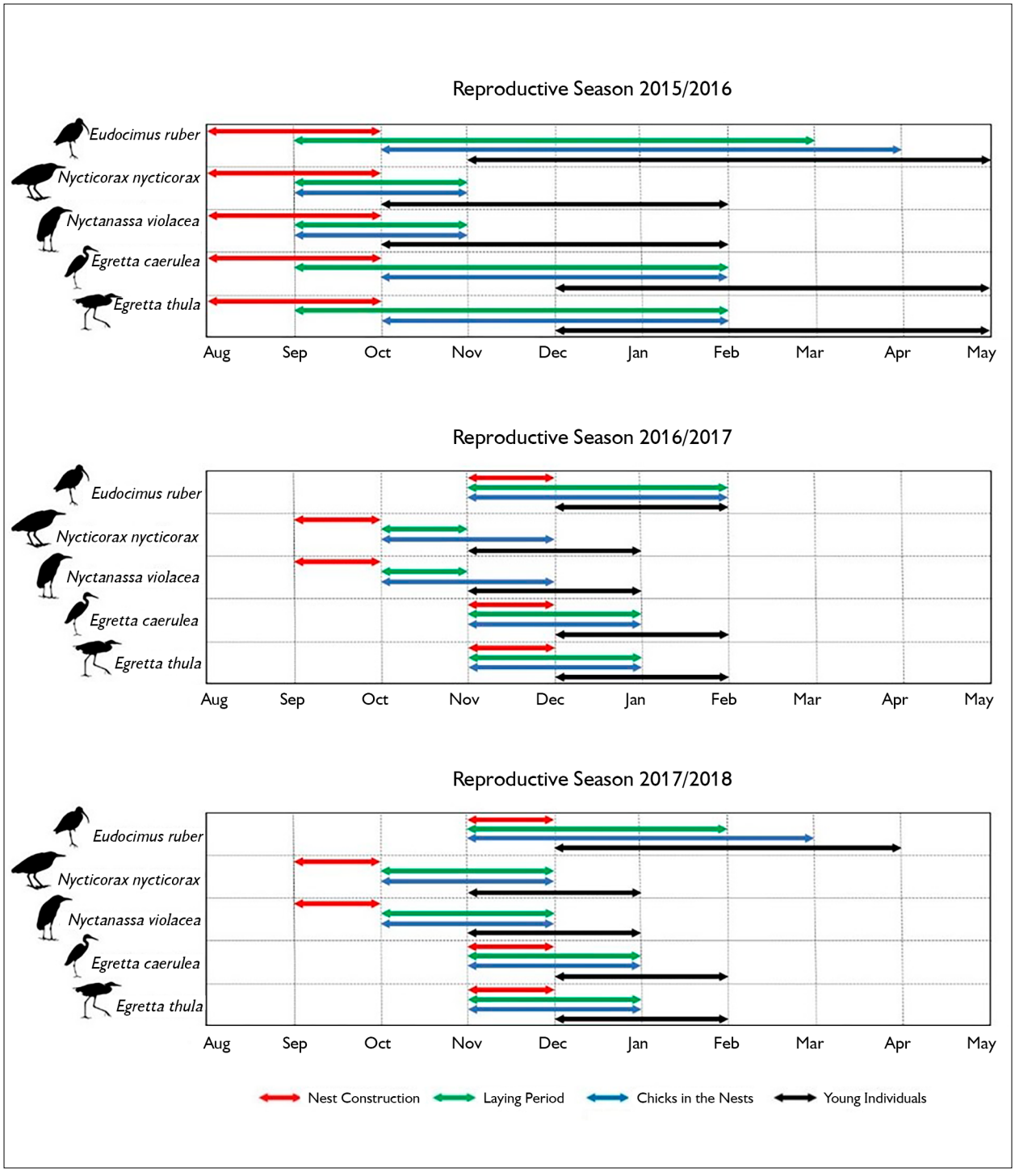

Figure 3. Periods of nest construction (red arrows), egg-laying and incubation (green arrows), presence of chicks in nests (blue arrows), and presence of young outside the nests (black arrows) during the 2015/2016, 2016/2017, and 2017/2018 breeding seasons. Image: Henrique Chupil (2025).

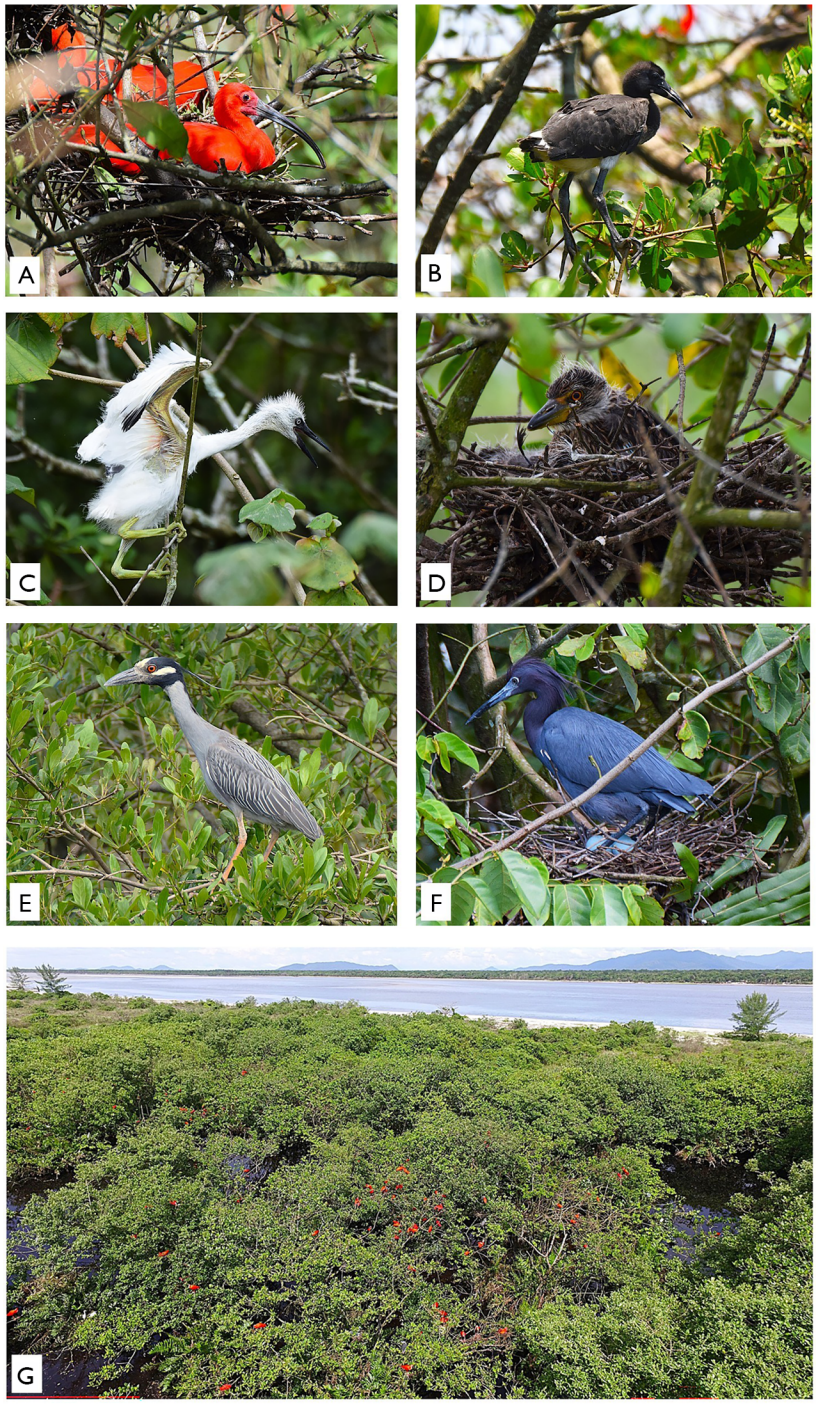

Figure 4. A) Scarlet Ibis at the nest; B) Scarlet Ibis chick; C) Little Blue Heron chick; D) Blackcrowned Night-Heron chick; E) Yellow-crowned Night-Heron; F) little Blue Heron at the nest; G) aerial image of Scarlet Ibises within the colony. Images: Authors (2016).

BEHAVIORAL INTERACTIONS

Few behavioral interactions were observed among the species and among the specimens, and these occurred only occasionally, typically in relation to competition for landing sites. Snowy Egret exhibited agonistic behavior primarily in response to direct pressure. Little Blue Heron were the most behaviorally active. Scarlet Ibis interactions were relatively rare and more discreet compared to other species. Most disputes were intraspecific, generally involving competition for nesting sites within the colony or for materials used in nest construction.

Two noteworthy reproductive behaviors were documented for Scarlet Ibis: (1) two different females feeding chicks in the same nest, and (2) biparental care. During the incubation period, males typically assumed responsibility for nest duties during the morning hours, while females remained on the nest during the afternoon. As nestlings approached the fledging stage, both males and females would leave the nest to forage.

Scarlet Ibis, Black-crowned Night-Heron, and Yellow-crowned Night-Heron showed no observable reaction to potential predators such as the Southern Crested Caracara (*Caracara plancus* (Miller, 1777)) and the Great Black Hawk (*Urubitinga urubitinga* (Gmelin, 1788)). Furthermore, no significant behavioral responses were recorded in reaction to UAV flights over the nesting areas. Among all species, only Scarlet Ibis demonstrated greater tolerance to human presence during egg incubation. In contrast, egrets were more sensitive to disturbance, leaving their nests when approached by humans or during UAV operations.

BEHAVIOR OF NESTLINGS AND CHICKS

Nestlings of all species exhibited similar behaviors, remaining mostly inactive and becoming active when adults returned to feed them. Little Blue Heron and Snowy Egret nestlings had difficulty moving through the vegetation and generally stayed close to the nest. Scarlet Ibis nestlings, in contrast, were more developed and moved through and above the vegetation with greater agility. Yellow-crowned Night-Heron and Black-crowned Night-Heron nestlings remained mostly within their nests, which were more robust than those of the other species.

In the presence of potential predators, all nestlings displayed defensive behavior by standing motionless in an upright position.

Chicks exhibited species-specific behavioral differences. Black-crowned Night-Heron and Yellow-crowned Night-Heron chicks were predominantly slow-moving or motionless, mirroring the behavior of adults. Snowy Egret and Little Blue Heron chicks were more active and engaged in more exposed behaviors. Scarlet Ibis chicks displayed similar levels of activity but with more agile movements, often using their wings to assist in leaping between branches. This behavior intensified when adults approached with food, occasionally resulting in short chases through the vegetation and brief flights.

Chicks were also observed attempting to feed from non-parental adults, though these attempts were unsuccessful. Toward the end of chick development, some individuals—after being fed—continued to chase their parents for additional food. In response, adults would leave the nest, fly up to 200 meters away, and return, still pursued by their chicks. During early flight attempts, the juveniles showed irregular and unstable flight, which gradually improved over time.

Across all species, chicks typically remained still or made only minor movements, with significant activity occurring primarily during adult feeding visits.

Before dispersing from the nesting colony, Scarlet Ibis chicks formed small groups and made short flights around the area. After leaving the colony, they remained grouped, primarily on nearby mudflats off Cananéia Island. For the other species, departure from the colony was gradual and occurred as the chicks became capable of sustained flight.

DISCUSSION

The breeding species recorded in the colony are typical of estuarine environments in the Parque Estadual Ilha

do Cardoso (Chupil & Monteiro-Filho, 2022) and the municipality of Cananéia (Chupil, 2019). However, breeding activities in the region are noorly documented, with notable contributions by Noguchi (2015) and Paludo et al. (2018). Residents of a local village (Pontal do Leste) near the colony report that the nesting area was often used by a large number of egrets and herons as nesting and dormitory sites before 2014. Only in 2014 Scarlet Ibis started to visit and used the site for resting and breeding. Our records of six actively breeding bird species in the same nesting area reflect the typical colonial behavior described for most species in the Ardeidae and Threskiornithidae families (Kushlan & Hancock, 2005). During the 1900s, there was a significant decline in records of the Scarlet Ibis along the southern and southeastern coasts of Brazil. It was only in the early 1980s that Scarlet Ibis numbers gradually began to increase (Chupil & Monteiro-Filho, 2018). Reports of breeding events came eight years after the Scarlet Ibis was first sighted in the municipality of Cananéia (Chupil & Monteiro-Filho, 2018). The presence of Scarlet Ibises likely induced changes in the previously dynamic spatial use by other species, as residents near the nesting area reported that egrets and herons were predominant nesters before 2014 (Wellington das Neves, personal communication, 2015). With the arrival of the Scarlet Ibis, the number of egrets nesting within the core area of the colony declined. Instead, egrets began nesting in the peripheral areas of the lagoon, a pattern we observed consistently across all three reproductive seasons. Similarly, Hass et al. (1999) at Ilha do Cajual (State of Maranhão, northeastern Brazil) and Olmos and Silva-Silva (2001) at Cubatão (State of São Paulo) reported a predominance of Scarlet Ibis nesting over other species in mixed colonies.

The length of the reproductive period varied across the monitored seasons. The 2015/2016 season was the longest, beginning as early as austral winter. In other seasons, herons started breeding in September, while other species began in November. The reproductive timing observed in the last two seasons seems to reflect a common pattern among most colonial bird species nesting in southern and southeastern Brazil. Similar reproductive period lengths have been documented by other researchers for Scarlet Ibis (Olmos & Silva-Silva, 2001, 2003; Grose, 2016), egrets (Olmos & Silva-Silva, 2002; Noguchi, 2015), and herons (Branco & Fracasso, 2005; Grose et al., 2014). The extended length of the 2015/2016 season may be associated with the recent arrival of the Scarlet Ibis to the colony. Most species were likely still adapting to new conditions imposed by the high density of Scarlet Ibis and possible environmental variations, both of which could influence bird physiology.

The dominance of Scarlet Ibis nests and their occupation of a wider area has previously been described by Olmos and Silva-Silva (2003) in the mangroves of Santos and Cubatão (southeastern Brazil), where high nesting density directly contributed to reproductive success. This behavior is primarily driven by the reduction in predation risk (Hamilton, 1971; Moraes & Krul, 1995), a strategy also effective for other colonial nesting species (Kushlan & Hancock, 2005). The earlier arrival of herons to the colony may reflect their preference for more sheltered nesting sites, as early-arriving species often have priority in site selection (Burger & Gochfeld, 1985; Kim & Koo, 2009).

Proximity to feeding areas is often considered a key factor in the selection of nesting colony sites (McCrimmon Jr., 1978; Frederick, 2002). In this study, during the reproductive period, most birds were observed foraging primarily in the Ararapira Channel, located 1-26 km from the colony. In contrast, after the reproductive period, a greater number of birds were observed foraging on mudbanks to the southeast and east of Cananéia Island, at distances ranging from 40 km from the colony

The alternating parental care observed in Scarlet Ibis during nest building, egg incubation, and chick rearing aligns with the general behavioral patterns described for the Ardeidae and Threskiornithidae families (Frederick, 2002). However, in this study, we observed greater parental segregation during incubation, with males tending to incubate more frequently in the morning and females more

in the afternoon. We also recorded alloparental care in chick feeding, likely performed by individuals that either did not reproduce that year or lost their offspring, as previously documented for the American White Ibis (*Eudocimus albus* Linnaeus, 1758) by Herring and Gawlik (2007).

We observed that adult Scarlet Ibises, when landing to feed their young, often did so at a distance, prompting the chicks to pursue them for food. Recently fledged chicks would chase through the branches and occasionally rely on their wings for support. This behavior is similar to Hoatzin (*Opisthocomus hoazin* Statius Muller, 1776) chicks, specie with claws on the tips of its wings (Sick, 2001). Over time, they began making short flights until they were capable of fully leaving the nest. We believe this behavior was selected to stimulate flight development in the young, gradually improving their motor skills and flight capabilities. The flight's incentive for rapid emancipation to youngs was observed in White-Ibis by Petit and Bildstein (1986), being related with increase survival chances outside the colony.

Behavioral interactions within the colony were generally discreet for most species, except for egrets. Agonistic behaviors are commonly observed among egrets during foraging, both intra- and interspecifically (Coelho, 2009), often linked to the defense of feeding sites (Moralez-Silva et al., 2010). In this study, we also recorded such interactions in a reproductive context, which may help explain the spatial segregation of egret nests. Scarlet Ibises exhibited only sparse agonistic interactions, primarily intraspecific, mostly involving competition for landing spots, as also reported by Vigário (2014) in the state of Paraná. The low incidence of conflict among individuals may be attributed to the dense use of vegetation and the close proximity of nests, both of which contribute to the reproductive success of the species.

In summary, the initial occupation of the colony by a large number of Scarlet Ibis individuals led to changes in colony dynamics and directly affected the abundance and spatial distribution of other species. This highlights the importance of long-term studies to better understand the ecological relationships underpinning the reproductive dynamics of colonial birds and to inform more effective management actions. Conservation measures for the studied colony should include the protection of mudbanks, which serve as essential foraging areas, and the regulation of tourism to minimize disturbances to bird activity both at the colony and foraging sites.

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AUTHORS' CONTRIBUTION

H. Chupil contributed to project administration, formal analysis, funding acquisition, conceptualization, data curation, investigation, methodology, resources, software, supervision, validation, visualization, and writing (original draft, review, and editing); C. N. Louzada contributed to investigation, resources, validation, visualization, and writing (review and editing); and E. L. A. Monteiro-Filho contributed to formal analysis, conceptualization, data curation, investigation, methodology, supervision, validation, visualization, and writing (review and editing).