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Reproduction and agonistic behavior of black skimmers (*Rynchops niger*) in a mixed-species colony in the Brazilian Pantanal

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ABSTRACT

Black skimmers (*Rynchops niger*) are colonial waterbirds in Nearctic and Neotropical regions. They often breed in mixed colonies with terns. This work analyzes the reproductive biology of skimmers within a colony including large-billed terns (*Phaetusa simplex*) and yellow-billed terns (*Sternula superciliaris*), located along the Cuiabá river in the Brazilian Pantanal, during July–September 2015. We focused on nesting parameters, timing of reproduction, nest survival, predation risk, and agonistic behavior. Skimmer nests ($n = 31$) were not aggregated ($R = 0.40$); mean nest distance was 6.91 ± 3.39 m. Incubation lasted on average 21.6 ± 1.6 days. Nest survival was low (3.2%) due to predation and abandonment, with the green iguana (*Iguana iguana*) as major predator of eggs. Aggressive behavior included chase and turn-off flights and mainly involved birds of prey (26.5%) followed by jabirus (*Jabiru mycteria*; 18.2%). The low number of nesting terns ($n = 3$), which can act as protector species, may have negatively impacted the fledging success of *R. niger*. Reproductive parameters and the complexity of behavioral interactions in such mixed colonies should be further studied in the Pantanal as model cases for ecological/ethological adaptations of colonial breeders under the impact of a seasonally fluctuating water regime.

Introduction

Black skimmers (*Rynchops niger*, Rynchopidae) are widely distributed along the Pacific and Atlantic coasts of the Nearctic and Neotropical regions (Zusi & Garcia 2017). In addition, they are found along all major river systems in continental South America, except for the southern cone, showing seasonal geographic movements between the reproductive and non-reproductive periods (Mariano-Jelicich et al. 2007; Mariano-Jelicich & Madrid 2014; Antas et al. 2016; Vieira 2017). During the non-breeding season, skimmers congregate in flocks of sometimes up to 12,000 individuals near estuarine and coastal areas, migrating from different breeding areas in South America (e.g. Mariano-Jelicich et al. 2007; Mariano-Jelicich & Madrid 2014).

In mainland South America, black skimmers usually nest on sandy beaches or riverine islets in the Amazon and Pantanal river systems, often together with large-billed (*Phaetusa simplex*) and yellow-billed terns (*Sternula superciliaris*) (Sternidae) (Zarza et al. 2013; Antas et al. 2016; Vieira 2017). In the wetlands of the northern Pantanal in Brazil, their reproduction starts

with the onset of the dry season between April and June, when skimmers and terns gather at nesting sites to form mixed breeding colonies (Gwynne & Ridgely 2010; Zarza et al. 2013; Antas et al. 2016). Based on the variation of inundation and climatic effects, breeding colony sizes may fluctuate considerably in consecutive years (Antas et al. 2016). Skimmer nests consist of simple, shallow scrapes in the sand, with neighboring nests usually being located a few meters from each other (Zarza et al. 2013; Antas et al. 2016; Vieira 2017).

Mixed-colony breeding in waterbirds is a widespread strategy to enhance nesting success by reducing nest losses through predation and other disturbance events (Lemmetyinen 1971; Coulson 2002). In contrast to some coastal-breeding gulls (Laridae) and terns that form single-species colonies (Kruuk 1964; Burger & Gochfeld 1990; Fasola & Canova 1991; Velarde 1999), mixed breeding of skimmers and terns may be advantageous for the breeding partners (e.g. Lemmetyinen 1971; Erwin 1979; Pius & Leberg 1998). Colony breeders have developed a variety of strategies to optimize reproduction. For example, breeding synchrony is an important

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factor for mutualistic defense (Fuchs 1977; Gochfeld 1980). According to the "predator avoidance hypothesis," colonially breeding individuals may reduce the risk of nest predation by nesting near the center of the colony (Hamilton 1971) or by increasing joint defense (*cf.* Darling 1938; Kruuk 1964; Hoogland & Sherman 1976; Götmark & Andersson 1984). Anti-predator aggression has been documented for both skimmers and terns, which often breed in large colonies, either conspecifically or mixed with two or more species, and they may form swarms in the presence of potential predators that will be attacked in aggressive encounters (e.g. Kruuk 1964; Erwin 1979; Burger & Gochfeld 1988, 1991; Groom 1992; Clode et al. 2000). Apart from defense aspects, colonial nesting may be beneficial for individuals since they can efficiently search for and exploit food resources by observing the foraging movements and success of nest neighbors (Krebs et al. 1972; Emlen & Demong 1975).

Predation may significantly affect the reproductive success of skimmer and tern colonies, but types of predators usually differ between inland and coastal populations. For example, a five-year monitoring of coastal-breeding black skimmers in New Jersey, USA yielded a variety of predators, including gulls, oystercatchers, and mammals, causing an annual loss of up to 50% of the colonies (Burger 1982). In Virginia, USA gulls (*Larus argentatus, L. atricilla, L. marinus*) were found to be the main predators on mixed skimmer-tern marine colonies (O'Connell & Beck 2003). In the Brazilian Pantanal, a variety of predators including mammals, birds of prey, and reptiles have been reported (Antas et al. 2016).

In the Neotropics, studies on skimmer-tern colonies have been directed mostly toward distribution and dynamics of coastal populations (e.g. Quintana & Yorio 1997; Mellink et al. 2007; Castillo-Guerrero et al. 2014), while breeding and behavioral aspects have rarely been analyzed in inland populations (Krannitz 1989; Zarza et al. 2013; Antas et al. 2016; Vieira 2017). Though distribution, coloniality, colony sizes, nest site fidelity, and breeding of skimmers have been recently studied for the focal region (Antas et al. 2016) and for some coastal populations (Vieira 2017), data on other reproductive parameters such as incubation, nest survival, and anti-predator behavior are so far missing for the Pantanal. This might be due to the aperiodic occurrence of breeding colonies that may exist at a specific site in one year but may not be maintained in subsequent seasons. Indeed, unpredictable changes in environmental conditions (e.g. inundation) strongly impact the availability and appropriateness of nesting sites, thus often forcing colonies to relocate (*cf.* Antas et al. 2016). Here we present for the first time detailed reproductive and

behavioral data on black skimmers within a mixed-species colony including large-billed and yellow-billed terns during a breeding cycle (July to September) in the northern Pantanal. Our study focused on (1) nest site characteristics, (2) incubation and timing, (3) nesting success and nest survival, (4) predation impacts on eggs and offspring, and (5) agonistic behavior against predators and other causes of disturbance. With respect to timing of reproduction and nest survival we considered the following working hypotheses: (1) Reproduction time is similar to that of other South American populations. However, given the specific conditions of the environment (i.e. onset of flooding), breeding time is shorter than in marine or inland breeding colonies of the Neotropics not impacted by a monomodal flood pulse. (2) As suggested by other studies (Burger 1982; O'Connell & Beck 2003; Brooks et al. 2014), the impact of avian and mammal predators, which have been identified as the main threats to eggs and young, should be greater than that of other predators. Likewise, diurnal predation may be predominant while nocturnal predation is of minor importance for skimmer-tern breeding colonies.

Materials and methods

Study area

The Pantanal Biome in Brazil, Bolivia, and Paraguay is one of the most important inland aquatic ecosystems in the Neotropical region and comprises the largest floodplain in the world (Alho et al. 1988; Junk et al. 2006). Its wetlands are within the southern-central breeding range of *R. niger, P. simplex*, and *S. superciliaris* (Gwynne & Ridgely 2010; Antas et al. 2016). We carried out our study from 12 July to 15 September 2015 at Praia do Totelão (16°32′ 11.10″S, 56°23′58.20″W), a 11,500 m^2 exposed sandbar (414 m long × 51 m wide at start of study; extension varies with season, with average area size 0.5 ha; Antas et al. 2016) along the Cuiabá river, 200 km southeast of the city of Cuiabá, Mato Grosso, Brazil (Figure 1). The study area is part of the Reserva Particular do Patrimônio Natural (RPPN) SESC Pantanal, which extends over 1000 km^2 in the Poconé subregion of the northern Pantanal in southwestern Brazil, adjacent to the border with Bolivia (Antas et al. 2016). During the study period only a few plants were found on the sandbar, including grasses (Poaceae), alluvial macrophytes such as *Eichhornia crassipes* and *E. azurea* (Pontederiaceae), and a sparsely scattered low vegetation of flood-resisting herbaceous plants (height
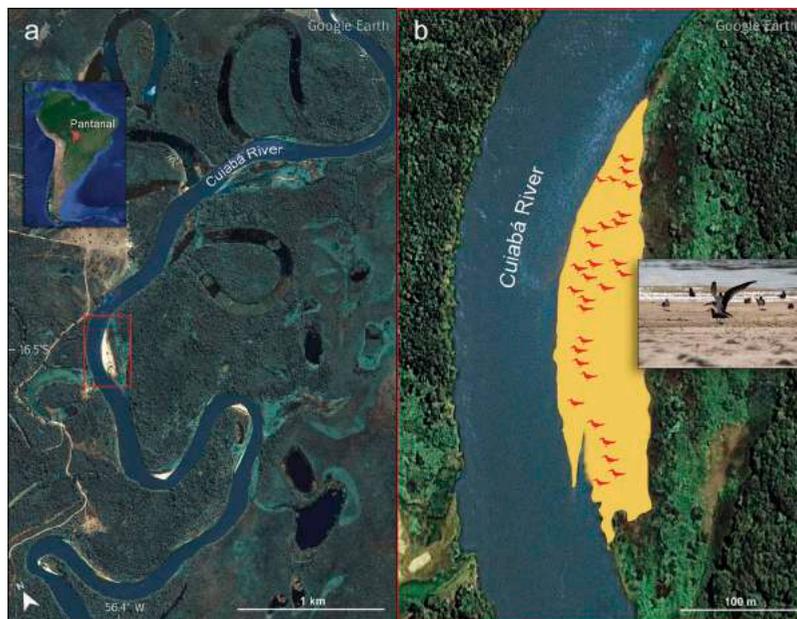
Figure 1. Pantanal study area: (a) at Praia do Totelão; (b) Cuiabá River, northern Pantanal, Mato Grosso, Brazil.

0.5–3 m) occurring at the peripheral area behind the boundary of the sandbar.

Data collection and observations

The survey of the colony started when breeding had already begun (*sensu* Antas et al. 2016; *R. niger* breeding starts usually in May in the study area). In order to cover activities within the colony during different daily phases, the observation hours were alternated daily. On one day observation times were in the period 06:00–09:00 h and 11:00–14:00 h, while on the next day they were changed to 06:00–11:00 h and 14:00–17:00 h. Nocturnal observations were made twice per week. However, since brooding or resting birds responded strongly to nocturnal observer activities and flashlight disturbances, night observation times were restricted to 2 hours after sunset (17:40 h) and 2 hours before sunrise (05:30 h). Total observation time was 410 hours.

Because of specific observation demands (e.g. adult brooding behavior, displays, activity patterns of precocial offspring) two observation hides (Wildlifephotography®, http://www.wildlifephotographyshop.com) were placed 5–10 m away from the margins of the colony. These tents were equipped with large viewing windows on each side. While the camouflage effect of the outside material helped us to closely approach the colony, the dimensions of 142 cm (length) and 168 cm (height at center) allowed two-person observations. The tents were established on the first day of the survey (10 August) before sunrise. The first tent was located in the northern part of the sandbar and the second one in the southern part of the study site. Observation distances to individual nests varied between 22 and 65 m, and the position of tents was adapted to specific observation demands during the progress of reproduction phases, e.g. display behavior, adult brooding behavior, activity patterns of precocial chicks, and predation monitoring.

Observations were conducted by means of a spotting scope (KOWA PROMINAR TNS-3 with 77 mm objective lens and 40–60× optical zoom), binoculars (Nikon Sporter EX 10 × 50). Behavior was recorded with a camcorder (Panasonic HC-V550, 52× optical zoom). For the 24/7 monitoring of behavioral interactions within the colony, and for recording of predation events, three wildlife cameras were placed to survey the central, northern, and southern parts of the sandbar. Given the absence of bushes and trees, they were fixed on wooden posts at 50–80 cm above the ground and set to record 30-second videos (in 24/7 mode). Two different models of automatic cameras were used: one Bushnell Trophy Cam HD Aggressor, 1920 × 1080 pixels, 32 GB SD card; two UWAY VH400, 1280 × 720 pixels, 32 GB SD card. The cameras were able to detect movements as well as changes in body temperature by an infrared sensor, and started to record only if both factors were present at the same time. Moreover, both cameras worked with no-glow black LED night vision flash for invisible flashlights. The UWAY cameras also had a color display for live preview and video playback, to check the videos directly in the field. With each recorded video

sequence, the vocalizations of the passing object, together with the date, time, and temperature, were stored automatically.

To obtain a complete set of data it was necessary to change SD cards and batteries of each camera trap once a week, together with those of the sound recorder. Subsequent to the maintenance, all collected data were directly saved on a laptop computer and on external hardware. In the course of the study, camera traps were moved to different nesting locations depending on the individual stages of brooding and hatching activities of individuals.

Nest identification and spatial analysis

In order to collect individual datasets for breeding pairs and to avoid observation replications, each nest site was marked with a small, numbered identification flag: nests of *R. niger* with red-green, those of *P. simplex* with yellow, and those of *S. superciliaris* with blue flags and a letter for the location (N = north, S = south). The location of each nest site was recorded by a Garmin GPS 12 and a Garmin 78S to analyze nearest-neighbor distances and spatial nest segregations.

Nest density was calculated from the number of registered nests divided by the sampled area size. Registered nest sites were mostly located in two different areas of the sandbank, the northern and the southern part. Therefore the study site was separated into two subcolonies, and spatial parameters were calculated for each subcolony as well as in total.

To determine the patchiness of nests, the Aggregation Index (R) was calculated. Nearest-neighbor distances (NNDs), as well as distances of the nest from the river, were determined and calibrated using Google Earth. Following Clark and Evans (1954) the Aggregation Index (R) was calculated by dividing an observed distribution (r_A) by a random distribution (r_E), with N = total number of nests and p = the density of the observed distribution expressed as the number of individuals per unit of area:

$$R = r_A/r_E \qquad (1)$$

$$r_A = \sum r/N \qquad (2)$$

$$r_E = 1/2\sqrt{\rho} \qquad (3)$$

To compare the two distributions statistically the standard variate of the normal curve (c) was used (t-test, two-tailed; significance level = 0.05):

$$C = r_A - r_E/\sigma r_E \qquad (4)$$

$$\sigma = 0.26136/\sqrt{N\rho} \qquad (5)$$

The outlines of the sandbank were recorded with Garmin 78S. Subsequently, datasets were converted with DNR Garmin (version 5.4.1). GE-Path (version 1.4.5) was used to calculate the square footage of the sandbank. By using geographical coordinates, nesting maps were assembled with Google Earth (version 7.1.5.1557).

Incubation and hatching

Established nest sites were registered, and thereafter inspected every second day. New nests were considered active when they contained one or more eggs and when active incubation was observed. After hatching, the young were color marked (small ventral plumage color mark) for individual recognition.

Monitoring of anti-disturbance and anti-predator interactions

We noted disturbance and predation events, type of predator, and anti-predator response for all three species. Black skimmers and terns are known to use different flight strategies in response to intruders approaching the colony (e.g. Lemmetyinen 1971; Erwin 1977; Burger & Gochfeld 1991; Groom 1992). Apart from "fly-bys" or "long-passing" with no direct attacks (for definition, see Burger & Gochfeld 1991), aggressive flights reflect the highest level of aggression, with aerial maneuvers toward the target such as conspecifics, heterospecifics, potential predators (including all birds of prey), and human intruders. Based on the classification of Burger and Gochfeld (1991) three types of flight attacks can be defined in skimmers and terns: (1) "Chase": repeated overflights of approaching aggressors but without specific attacks such as dives or turn-offs; (2) "Dive": repeated flights over the aggressor and then turning down steeply at an increased speed closely approaching the intruder, rarely striking it with the bill or feet and usually rising again shortly before a collision; and (3) "Turn-off": intruders are approached laterally with abrupt directional changes of flight direction in front of them. In each case we recorded the species involved, individual attacking pair, and duration of the attack, which was classified as "short" (0–30 seconds), "medium" (> 30–120 seconds), or "long" (> 120 seconds). Additionally, the phase of the breeding cycle (incubation, hatchling, fledgling) and the day within this period were documented. Whenever possible, avian intruders or aggressors

were identified with the help of Gwynne and Ridgely (2010). Due to flight speed, raptors could sometimes be identified only to family level; in such cases, we simply referred to them as "birds of prey" (see Table 1).

Regarding targets of flight attacks, disturbances of the colony responded to by one or more members were categorized into four classes: intraspecific, interspecific, predator-specific, or human-influenced. "Intraspecific disturbance" was defined as any event involving a conspecific individual, no matter if nesting on the sandbar or just overflying. "Interspecific disturbance" referred to encounters between any of the three colony species and/or other heterospecifics with no predatory impact on the colony breeders. "Predator-specific disturbance" involved any potential predator of the colony breeders. Finally, "human-influenced disturbance" included either active disturbance by direct human approach (i.e. observers) or indirect disturbance caused by the permanently installed equipment on the sandbar. Whenever possible, behavioral characteristics and interactions were videotaped.

Data analysis

Statistical analyses were performed using the program GraphPad Prism (GraphPad Software, Inc.). For nesting parameters, a one-way analysis of variance (ANOVA) was applied to approximately normal-distributed data (significance level $p < 0.05$). Following

Table 1. Number of attack flights ($n = 132$) of four black skimmer (*Rynchops niger*) pairs against intruders, potential predators, and human observers at Praia do Totelão, northern Pantanal, Mato Grosso, Brazil during a complete breeding cycle from August to September 2015, related to duration of attacks (short: 0–30 seconds; medium: > 30–120 seconds; long: > 120 seconds). Intraspecific disturbance: by other *R. niger* colony members; interspecific disturbance: by colony members large-billed (*Phaetusa simplex*) and yellow-billed terns (*Sternula superciliaris*), and by southern screamer (*Chauna torquata*). Herons included cocoi heron (*Ardea cocoi*) and other species (unidentified). Birds of prey included roadside hawk (*Buteo magnirostris*), great black hawk (*Buteogallus urubitinga*), southern crested caracara (*Caracara plancus*), osprey (*Pandion haliaetus*), and other species (unidentified). Vultures included black (*Coragyps atratus*) and lesser yellow-headed vultures (*Cathartes burrovianus*). Disturbance by human observers included control/ maintenance of recording equipment and access to observation tents.

Source of disturbance/Predator	Short	Medium	Long	Total
Intraspecific	5	3	–	8
Interspecific	5	3	–	8
Heron	12	3	6	21
Jabiru	4	18	2	24
Bird of prey	24	7	4	35
Vulture	10	3	3	16
Green iguana	–	2	–	2
Human observers	6	7	5	18
Total	66	46	20	132

each ANOVA, a Tukey's multiple comparison test was carried out to compare mean values.

The daily survival probability (DSP) of eggs and hatchlings, and nest survival, were calculated with the Mayfield (1975) method: DSP = total number of failed nests ÷ total number of exposure days. Hatching and fledging success were calculated using Erwin's (1979) method: hatching success = number of hatchlings ÷ total number of eggs; fledging success = number of fledged chicks ÷ total number of nests.

For the comparison of agonistic responses of pairs during different phases of the breeding cycle, a Kruskal–Wallis test ($p < 0.05$) was used.

Results

During our observations of the study colony, the number of breeding *R. niger* pairs outnumbered by far that of the two tern species (*S. superciliaris*: $n = 2$; *P. simplex*: $n = 1$). Since the sampling size for the latter two species was too low for statistical comparison, we considered only nesting, breeding, and behavioral data of *R. niger*. A total of 31 nests were registered within the study area, averaging 0.27 nests per 100 m². The study area consisted of two spatially separate colony sites (northern/southern site of beach), 33 m apart from each other. The resulting areas provide a breeding area of 4073 m², with a density of 0.47 nests per 100 m² in the northern, and 5127 m², with a density of 0.23 nests per 100 m² in the southern part. Most of the nests were close to the riparian site and approximately 0.5 m above water level.

Nest site and nesting parameters

In the phase of nest site selection, the high number of skimmers did not allow for a reliable distinction between individual pairs because the birds were not marked. Nests were shallow scrapes on bare sand (unlike the terns, which nested near debris or alluvial macrophytes). Of the 31 nests of *R. niger* found at the start, 29 were included in the nest site analysis, of which 18 were located in the northern part and 11 in the southern. The remaining two nests had to be excluded, since one with a young already hatched at the beginning of the study period was changed in position by the parental birds almost every day. A second nest was excluded because of a malfunction of the handheld GPS. The nests were not aggregated in the overall study area ($R = 0.40$, c = − 12.3, $p > 0.05$), nor in the subcolonies (north: $R = 0.35$, c = − 13.45, $p < 0.05$; south: $R = 0.39$, c = − 2.52, $p > 0.05$).

Overall NND was 6.91 ± 3.39 m (range, 2.88–15.60 m) and significantly larger in the southern part (9.13 ± 2.46 m vs. 5.75 ± 3.22 m in the northern part; two-tailed *t*-test, *p* = 0.006). Distances from the nests to the river also differed significantly between the two sub-colonies (two-tailed *t*-test, *p* = 0.01), with 7.07 ± 3.50 m in the southern part and 11.89 ± 5.55 m in the northern. Overall, a mean distance of 10.23 ± 5.44 m (range, 0.91–21.24 m) was observed.

Egg laying and incubation

Rynchops niger laid eggs almost during the whole observation period. For the 31 surveyed nests, mean clutch size was 2.29 ± 0.92 eggs, varying from one to four eggs (n_{total} = 71 eggs). Based on the total nest number, three-egg clutches were most common (*n* = 13, 41.9%) followed by those with one or two eggs (each *n* = 8, 25.8%) and those with four eggs (*n* = 2, 6.5%). Incubation time was on average 21.6 (± 1.6) days (range, 19–24). Both males and females participated in incubation, the latter not being fed by males during this time (only during display and mating).

Hatching, fledging, and parental care

Due to predation and other events (for details, see next paragraph), a total of 18 young (25.3% of all eggs) hatched in only six nests (19.4%), two in the northern and four in the southern subcolony. The hatching process lasted less than one day. During the first day of hatching, chicks remained in the nest, brooded and guarded by a parent. On the second to third day after hatching, adults started to excavate new scrapes 1–2 m away from the original nest, and subsequently chicks moved to these new nest sites. At least one parent remained attending the nestlings until the fourth to fifth day. Afterwards, parents reduced their caring activities, and chicks were exposed to the sun in the early morning and afternoon for 2 to 3 hours since they were then able to regulate their body temperature.

Nest survival and loss by predation and abandonment

For the 31 nests under study, DSP was 88% for nests and 89% for eggs (*n* = 71). DSP for nestlings was 78%, while overall fledging success was 3.2%. Of the 18 hatchlings, 17 (94.4%) failed to reach the fledging phase. Only one chick successfully fledged by day 27, which means a total success rate of only 1.4%. Most of the eggs (*n* = 53, 74.6%) failed before hatching, either

through predation (*n* = 30) or nest abandonment (*n* = 23; Figure 2). Nests of all clutch sizes (1–4; *n* = 15, 48.4%) were predated before hatching, with an average of 2.42 ± 1.05 eggs (*n* = 30). Concerning loss by predation, three-egg clutches were most predated (*n* = 10, 76.9%), which was high above their percentage (*n* = 13, 41.9%) in total nests. On the other hand, four-egg clutches (*n* = 2) had the highest hatching success (*n* = 4) and a nest survival of 50%, followed by three-egg clutches (*n* = 12) with a nest survival of 30.8%, while one- and two-egg clutches failed completely in hatching.

During incubation, 13 nests (41.9%) were deserted, most of them for unknown reasons (*n* = 11). One nest with one remaining egg (of initially three eggs) was deserted after predation of two eggs by an iguana (see below); another (with three eggs) was abandoned due to observer-induced disturbance. During the hatchling phase, one nest with three chicks was deserted, and a chick from another nest disappeared for unknown reasons (likely by predation). One chick of a four-egg clutch died (for unknown reasons) after two siblings were predated by a roadside hawk (*Buteo magnirostris*); however, the remaining chick survived and successfully fledged.

Predation of eggs and young included a variety of predators (Figure 2, 3). Predation events were registered during both day and night, and included terrestrial and aerial predators of three main types: two reptile species (green iguana, *Iguana iguana*, Iguanidae; yacare caiman, *Caiman yacare*, Alligatoridae), one bird of prey (roadside hawk, Accipitridae), and one stork (jabiru, *Jabiru mycteria*, Ciconiidae) (Figure 3). At least three other potential avian predators, cocoi heron (*Ardea cocoi*, Ardeidae), great black hawk (*Buteogallus urubitinga*, Accipitridae), and southern crested caracara (*Caracara plancus*, Falconidae) were seen visiting, or passing near, the study colony; but we failed to record any direct nest predation by these species.

Although iguanas were not directly observed preying on nests nor recorded by our videotapes, their footprints were found at 16 different sites with robbed nests suggesting predation at dusk and dawn, even possibly at nights with full moon (Figure 4). Based on this evidence, iguanas presumably took 30 eggs and four chicks out of 16 clutches. In addition, many yacare caimans and their young were present on the sandbar during the complete breeding cycle. During the night they took at least three chicks of *R. niger* (recorded by camera traps). Almost every day a jabiru visited the study area, and it was once observed preying on a 7-day-old *R. niger*
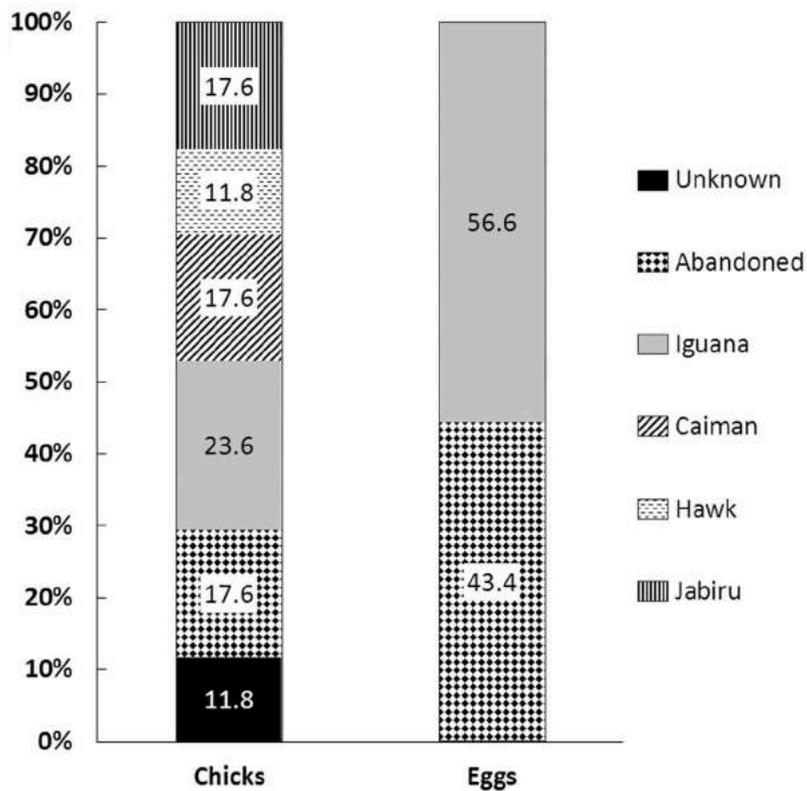
Figure 2. Percentage of egg (*n* = 53) and chick (*n* = 17) losses during the study period (July to September 2015) of *Rynchops niger* at Praia do Totelão, northern Pantanal, Mato Grosso, Brazil by predation records or other reasons. Note that egg loss was either exclusively caused by the green iguana (*Iguana iguana*) or by nest abandonment (for unknown reasons). Other predators included yacare caiman (*Caiman yacare*), roadside hawk (*Buteo magnirostris*), and jabiru (*Jabiru mycteria*).

chick (Figure 3d; altogether three chicks of the same clutch). Two further *R. niger* chicks were preyed on by a roadside hawk.

Aggressive behavior and anti-predator response

We recorded 132 incidents of aggressive (anti-disturbance) behavior against intruders and potential predators in five pairs of *R. niger* during the complete breeding season. Six sources of disturbance, including a variety of potential predators, could be identified (Table 1): (1) intraspecific (*R. niger* from the same colony); (2) interspecific (*P. simplex, S. superciliaris* from the same colony; southern screamer, *Chauna torquata*, Anhimidae); (3) potential and confirmed avian predators (birds of prey, herons, jabiru); (4) scavengers (vultures); (5) other potential (terrestrial) predators (iguanas) (Figure 5); and (6) human disturbance (by observers).

Two different types of aerial attack—chase attacks (predator-specific) and turn-off attacks (observer-induced, predator-specific)—were observed for *R. niger*, while dive attacks were noted only for both species of terns. Chase flights were 100% successful (e.g. the intruder left the colony without predation), while turn-off attacks had a success rate of 48%. Four pairs (R1–R4) attacked on average 24.8 ± 15.2 times (range, 11–46 times) during the complete breeding cycle; no significant difference (*p* = 0.29, Kruskal–Wallis) was observed between individual pairs in the frequency of attacks related to the period of breeding. However, there was a tendency toward more frequent attacks with the progress of breeding. While R1 could not be observed during the incubation period, R2 attacked on average 1.43 ± 0.99 times during incubation (*n* = 30) and 3.0 times (± 1.09) during the hatchling period (n = 15), R3 attacked 0.85 ± 0.94 times during incubation (*n* = 17) and 1.17 ± 0.50 during hatchling period (*n* = 7), while R4 attacked 0.46 ± 1.09 times during incubation (*n* = 10) and once (*n* = 1) during the hatchling period.

Attacks lasted on average 52.1 s (± 75.4). The duration of attacks was strongly dependent on the potential aggressor (Table 1, *n* = 132). The majority of responses toward birds of prey (68.6%, *n* = 35), herons (57.1%, *n* = 21), and vultures (62.5%, *n* = 16) were short, while medium responses were predominant toward jabirus
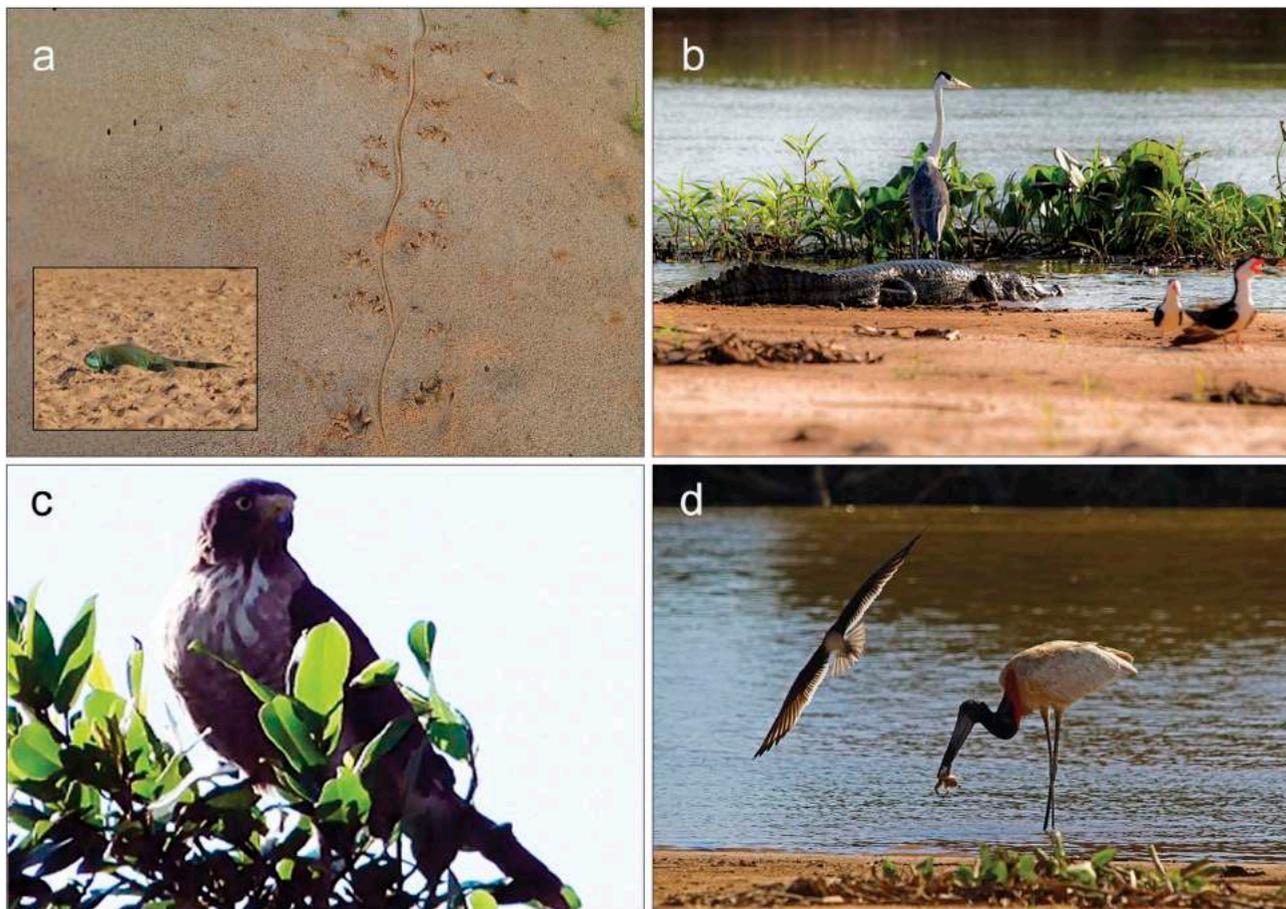
Figure 3. Predation of eggs and chicks of *Rynchops niger* at Praia do Totelão, northern Pantanal, Mato Grosso, Brazil by various predators during the 2015 breeding season. (a) Tracks around nest sites and on the sandbar indicating nocturnal predation by the green iguana (*Iguana iguana*); (b) yacare caiman (*Caiman yacare*) and cocoi heron (*Ardea cocoi*) at the riverside of the sandbar; (c) roadside hawk (*Buteo magnirostris*) on the lookout near the study colony; (d) Predation of a *R. niger* chick by a jabiru (*Jabiru mycteria*) (photos: INAU/CO.BRA).

(75.0%, *n* = 24) and, to a minor extent, toward human observers (38.9%, *n* = 18). Half of the observed attacks were short (50%), while 34.8% were medium, and 15.2% were long (Table 1). Attacks on human disturbers were fairly long (188.3 ± 88.2 s) while those on interspecific intruders were fairly short (23.3 ± 15.7 s). Birds of prey caused most incidents responded to by aggressive behavior (26.5%), followed by jabirus (18.2%), herons (15.9%), and human intruders (13.6%), while conspecifics (6.1%), interspecifics (6.1%), and iguanas (1.5%) were only occasionally to rarely involved.

Discussion

Timing of nesting, nest site characteristics, and nest building

Black skimmers have been described as arriving later at nesting grounds than terns, joining the latter to form mixed-species colonies, might be an active decision of skimmers *sensu* the "protector species hypothesis" (Pius & Leberg 1998). In contrast, another study on mixed colonies in the Pantanal (Antas et al. 2016) revealed that nesting (and its initiation) was triggered by the physical availability of open grounds such as riverine beaches or islets, depending on water level and social aspects, i.e. aggregation of larger groups in the course of the breeding season. However, the timing of reproduction depends strongly on the population origin. Across the Americas, breeding seasons vary considerably in length and time between one to six months (see overview in Antas et al. 2016; Vieira 2017). For example, in Brazilian Amazonia breeding was recorded between October and December (Krannitz 1989; Zarza et al. 2013), while in North American skimmers it lasted from May to August (Burger 1982; Dinsmore 2008). In our study, nesting had already begun before we started the survey in July and was not finished by September when we finished
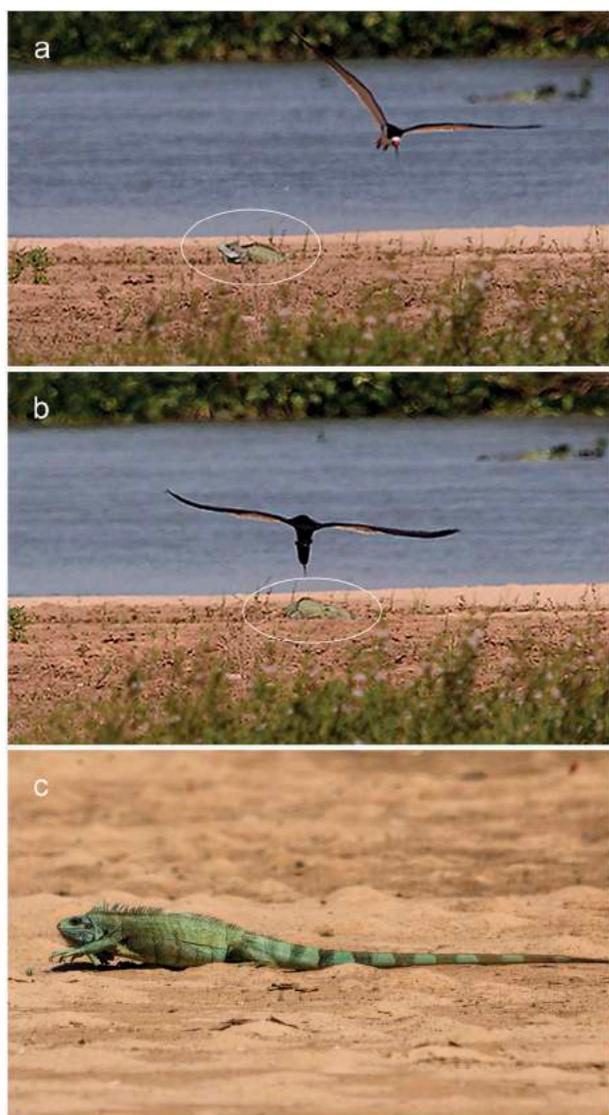
Figure 4. Aerial dive attack of a black skimmer male (a, b) toward a green iguana, *Iguana iguana* (c), approaching the nest site of the breeding colony at Praia do Totelão, northern Pantanal (photos: INAU/CO.BRA).

our fieldwork. However, as mentioned before, the species' presence and reproduction in the Pantanal (i.e. along the Cuiabá river) strongly depends on the level of inundation (Antas et al. 2016). In years with regular water levels (see average duration from 2002 to 2013), skimmers may occur from late April to mid November, with the onset of nesting in late May and two pronounced breeding seasons from May to July and from August to October. Therefore, under unfavorable ecological conditions (e.g. high water extending into the Neotropical winter), breeding may start only by late August and extend just until early October (Antas et al. 2016).

Skimmer nests and nest sites were similar to those described for the Pantanal (Antas et al. 2016) and for

Virginia, USA (Erwin 1979). A disadvantage of this nesting strategy could be the absence of any hiding options for the chicks, which are usually pressed to the ground between feeding intervals (Antas et al. 2016; this study). However, although chicks are well camouflaged by their sand-colored plumage, nests may be located close to vegetation or flood debris to enhance protection against predators (Antas et al. 2016).

NNDs, both for overall colony and for subcolonies, were lower than those for skimmers alone in mixed colonies within the study region (n = 8; mean = 9.8 m), but similar to that for overall NNDs (skimmers-terns) in such colonies (7.3 m) (Antas et al. 2016). However, mean NNDs in other colonies of the Nearctic and Neotropic regions were much larger, e.g. 28.5 m (n = 37) in Amazonian Brazil, Pará (Krannitz 1989), or even 192.1 m (n = 86) in coastal colonies in the eastern USA (Delaware, Maryland, Virginia) (Erwin 1977). Such differences may be best explained by the smaller sizes of the available breeding areas of the Cuiabá river colonies (0.54 ha [± 0.50] in 2012, 0.67 ha [± 0.64] in 2013; Antas et al. 2016) than the Amazonian colony (400 ha).

Incubation

The determined incubation period was shorter than that of some *R. niger* populations, thus supporting our working hypothesis 1, but still within the overall range reported for the species (Vieira 2017; Zusi & Garcia 2017). However, it was longer than that reported for Brazilian Amazonia, with the restriction that just two nests were included (each 20 days) (Krannitz 1989). For a colony in Mississippi, USA, 22.7 (± 2.5) days were recorded (May) (Dinsmore 2008), while 28 days were found for Peru (September) (Groom 1992). These fall into different seasons (Nearctic spring/summer vs. Austral winter/spring), despite the fact that average temperatures during day and night were fairly similar. The difference in the incubation time recorded for the Peruvian colony (Groom 1992) could have been caused by different observation methods. While we found that skimmers laid one egg per day, Groom (1992) estimated one egg every two days.

Daily survival probability and success rates

DSP for eggs in the northern Pantanal was lower than in Brazilian Amazonia (98%, Krannitz 1989) and in Virginia, USA (93.8%, Brooks et al. 2014). Hatching success (21%) was similar to that in Virginia (17%,

Keller 1992), but much lower than for another population in Virginia (79%) (Erwin 1977) and that in Amazonia (85%) (Krannitz 1989). However, both Erwin (1977) and Krannitz (1989) mentioned that no predation events were observed, in strong contrast to our study where predation had a huge impact on egg and chick survival. For Amazonian skimmers, parental care observed was similar to that in the Pantanal colony (Krannitz 1989).

The overall hatching success of our mixed-species colony (including *R. niger*: n = 71, 25.3%; *Phaetusa simplex*, n = 3, 100%; *Sterna superciliaris*, n = 5, 100%) was 32.9%, which is lower than in a Peruvian colony of the same three species in two consecutive years (62% and 42%) (Groom 1992). There, hatching success was positively correlated with the number of individuals present in two consecutive breeding seasons (n = 1533 and 1795) (Groom 1992). The low number of breeding pairs and the resulting low nest densities could be one explanation for the low hatching rate noted during our study.

Fledging success was similar to a colony in New Jersey, USA (1%) (Burger 1982) and two RPPN colonies in 2012 and 2013 (< 1%) (Antas et al. 2016); however, it was much lower than for skimmers in Virginia, USA (37%) (Erwin 1977). Fledging success may vary considerably between different years (Burger 1982; Brooks et al. 2014). In the overall study region, it may depend on nest desertion, predation, disturbance by humans, or unfavorable temperatures (Antas et al. 2016).

Predators and their impact

Our work presents the first quantitative-qualitative study on predation for a Neotropical inland mixed skimmer-tern colony, revealing a high predation impact on the nesting success of the surveyed species by different types of predators. Given the fairly high proportion of caimans and iguanas involved in predation events (54.8% of all nests), our results are in contrast to those of Groom (1992), who found that reptilian predators, such as iguanas and snakes, had only a minor impact (6%) on brood losses in a mixed skimmer-tern colony on the Manu river, Peru. In addition, the spectrum of predators reported here differs slightly from that of another study comprising the entire RPPN SESC Pantanal (Antas et al. 2016). The absence of mammal predators from our study site was perhaps due to the permanent presence of human observers at the sandbar.

Our study provides the first quantitative data for the green iguana as a main predator of eggs and chicks in a seabird colony (*cf.* Figure 2). Usually these lizards are considered to be herbivores, especially the older adults, which mainly consume leaves and fruits, but rarely animal food (carrion, invertebrates) (Alberts et al. 2004). However, in another study on an arboreal avian colony in the Pantanal, the green iguana was regularly observed to prey on eggs (Silva et al. 2000). Another new a predation record is from a jabiru feeding on a *R. niger* chick.

A possible explanation for the differing egg versus chick losses due to different predators could be the feeding activities of *R. niger*. Since skimmers catch fish even during the night (e.g. Robert et al. 1989; Cueva & Fernández 1996; Yancey & Forys 2010), when iguanas were also active (M. Hegmann & M. Schley, pers. obs.), we observed that clutches remained unattended for several minutes when both adults were foraging. Iguanas were seen during dusk, dawn, or at full moon crossing the sandbar, and it seems likely that they can track down eggs during bright tropical nights. Apart from iguanas, both adult and young caimans were observed when hunting for chicks (17.6%; Figure 2), with at least three successful attacks (all concerning the same nest on consecutive days). Nevertheless, as recently shown for bird communities in the Everglades, Florida, USA (Burtner 2011; Nell et al. 2016; Burtner & Frederick 2017), co-existence with alligators may be otherwise beneficial for colony-breeding waders since they can act as protector species deterring other predators such as snakes and mammals.

Compared with the impact of reptiles (54.8%) on nest survival, avian predation had only a minor impact (6.5%) at the study site (*cf.* Figure 2), which contrasts to working hypothesis 2. Unlike in marine habitats, gulls, as the main avian predators on coastal populations of seabirds, were absent from the surroundings of the study colony. However, we noted for the first time the jabiru preying on chicks of terns. Within this context, it was interesting to observe that the jabiru did not prey on freshly hatched chicks but was apparently waiting for older ones leaving the immediate nest area and approaching the river's edge. This behavior could be due to the more intensive defense of hatchlings in or near the nest by their parents, but also by learning effects, e.g. that older chicks represent a more substantial prey than young ones.

High nesting densities in colonially breeding seabirds can both favor a decrease in predation and enhance nest survival (e.g. for lapwings: Berg et al. 1992; for terns: Quintana & Yorio 1997; Lombard et al. 2010). Hence the low density of breeding pairs, especially terns, found in our study could partly explain the high predation rates observed. Apart from directly

causing nest losses, the high density of lizards (10 nests) on the sandbar might have been another reason for the high rate of nests abandoned during the study.

The specific conditions at the sandbar apparently strongly impacted the breeding success of the colony. In particular, the local combination of factors negatively correlated with breeding success, such as small number of pairs and/or aggressive individuals among terns, low nesting densities, and strong presence of diverse predators, contributed to the low hatching and fledging rates observed during the study.

Aggressive behavior and anti-predator response

Since open-ground breeders face higher predation risks to eggs and young than cavity nesters, they may respond in different ways toward potential predators (e.g. Clode 1993; Martin 1993), including flexibility in ecological adaptations over time (for review see Lima 2009). Firstly, the masking of nest sites and eggs and chick camouflage plumage prevent diurnal nest robbers from easily finding the nest site. Secondly, mobbing has been developed as a common strategy of aggressive response, often used in colonially breeding seabirds to divert potential predators away from nesting sites (e.g. Kruuk 1964; Burger & Gochfeld 1988, 1991; Clode et al. 2000; cf. Altmann 1956; Alcock 1998). Within mixed-species colonies, aggressive protector species such as gulls or terns may be "used" by less aggressive species such as R. niger (Lemmetyinen 1971; Erwin 1979; Pius & Leberg 1988). According to this theory, the overall defense situation of a colony would be strongly dependent on the population size of such a protector. In our case, however, the lack of a sufficient number of breeding pairs of terns in relation to R. niger may partly explain the low overall breeding success, yet with the reservation that such behavior is mainly directed at diurnal mammal or avian predators and may fail with regard to nocturnal predation.

The type and intensity of responses (i.e. flight attacks) toward intruders by terns and skimmers may depend on a variety of factors including species, approach distance, colony density, type of intruder, and even habitat type (Erwin 1979; Burger & Gochfeld 1988, 1990, 1991; Groom 1992). The analysis of frequency and duration of flight attacks regarding different types of disturbance (e.g. human-influenced, interspecific, intraspecific, predator-specific) in the studied colony yielded no significant differences in response to different aggressors. Nevertheless, the analysis of frequency and duration of attacks within the whole breeding colony showed that there was a significant difference between the number of attacks against human-influenced and predator-specific disturbances. This is plausible, because human disturbances were caused by the installation of equipment. Despite the permanent presence of the latter, the birds only attacked people on the day of establishment, suggesting that they became used to the daily visits of human observers. Thereafter, skimmers mostly did not even attack them—perhaps because they entered the colony through vegetation and were only briefly visible. In contrast, potential predators that approached from the water and were perfectly visible and/or close to the nesting grounds, were attacked with a much higher intensity. Even though not significantly different, there were slight tendencies for R. niger to attack more frequently during the hatchling period than during the incubation period. This is concordant with other studies indicating significant shifts in seabird behavior between the different breeding stages, e.g. that aggressive behavior of adults was higher during the hatchling period than during the incubation period (Lemmetyinen 1971; Brunton 1990; Whittam & Leonard 2000). Moreover, parental defense intensity in species with precocial young is expected to peak at hatching before decreasing again until fledging (Brunton 1990). Such a decrease in aggressive behavior was also recognizable in our data. However, given that only one chick of R. niger reached the fledging period, the results should not be over-interpreted.

An explanatory approach to the distribution of attacks during the breeding cycle assumed that the decrease from hatching to fledging is related to the need for both parents to forage, therefore leaving the colony less guarded by adults (Shealer & Burger 1992). Another assumption is that parents may abandon the colony when chicks have been predated or have died of other causes (Shealer & Burger 1992).

Conclusions

Apart from general approaches (e.g. Vieira 2017) or surveys (Antas et al. 2016), detailed studies on brooding and reproduction behavior of R. niger in the southern breeding grounds were lacking prior to this work. This might be not only due to the unpredictable environmental conditions of the nesting sites, but also to logistic restrictions on the observer side (i.e. assessment of appropriate study period; difficult transportation and installation of equipment due to remoteness of study areas; extensive and costly organization of research stays). However, mixed skimmer-tern colonies represent an appropriate example for assessing the impact of different ecological pressures on the reproduction and survival of colony breeders in seasonally

fluctuating microhabitats. Comparison with results obtained from colonies in North and South America (e.g. Krannitz 1989; Groom 1992; Dinsmore 2008; Zarza et al. 2013; Antas et al. 2016) revealed that both seasonal and local conditions strongly affect timing of reproduction, nesting and breeding parameters, and reproductive success in the involved species. Although skimmers and terns may respond in different ways to varying negative environmental impacts (e.g. flooding, predation), our study indicates that colony size may be a crucial factor for the nest survival of all members (*cf.* Antas et al. 2016), especially in view of the locally observed excessive predation. Compared with shoreline or offshore bird assemblages, inland colonies, such as the one studied in the Pantanal, are often small (i.e. due to area sizes), and breeding grounds may change between seasons in response to environmental pressure, such as flooding (Antas et al. 2016). Therefore, multi-year studies are hard to undertake, and the comparability of such breeding sites is low.

In contrast to coastal mixed-species colonies, where nest robbing by birds (e.g. gulls, raptors) is predominant (e.g. Hatch 1970; Fuchs 1977; Clode et al. 2000; see working hypothesis 2), we found that large-bodied lizards can be locally opportunistic (main) predators of eggs and chicks. Moreover, reproductive success may depend on the proportion of pairs of aggressive (e.g. terns) versus less aggressive species (e.g. skimmers) within the same colony. If the latter outnumber the former (as in our case), overall hatching and fledging success within a colony may be lower than if their ratio were more balanced. It is recommended that such correlations, as well as breeding site fidelity, be further analyzed in the Pantanal and elsewhere in the species' range.

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References

Alberts A, Carter R, Hayes W, Martins E, editors. 2004. Iguanas: biology and conservation. Berkeley (CA): University of California Press.

Alcock J, editor. 1998. Animal behavior: an evolutionary approach. Sunderland (MA): Sinauer Associates.

Alho CJ, Lacher TE, Gonçalves HC. 1988. Environmental degradation in the Pantanal. Bioscience. 38:164-171.

Altmann SA. 1956. Avian mobbing behavior and predator recognition. Condor. 58:241-253.

Antas PTZ, Carrara L, Kulaif-Ubaid F, Borges-Junior S, Pinheiro-Ferreira L, editors. 2016. Conhecendo o Pantanal, no. 10: Aves coloniais da Reserva Particular do Patrimônio Natural SESC Pantanal. Rio de Janeiro (RJ): SESC, Departamento Nacional.

Berg Å, Lindberg T, Källebrink KG. 1992. Hatching success of lapwings on farmland: differences between habitats and colonies of different sizes. J Anim Ecol. 61:469-476.

Brooks GL, Sanders FJ, Gerard PD, Jodice PG. 2014. Daily survival rate for nests of Black Skimmers from a core breeding area of the southeastern USA. Wilson J Ornithol. 126:443-450.

Brunton DH. 1990. The effects of nesting stage, sex and type of predation on parental defense by Killdeer (*Charadrius vociferous*): testing models of avian parental defense. Behav Ecol Sociobiol. 26:181–190.

Burger J. 1982. The role of reproductive success in colony-site selection and abandonment in Black Skimmers (*Rynchops niger*). Auk. 99:109-115.

Burger J, Gochfeld M. 1988. Defensive aggression in terns: effect of species, density, and isolation. Aggress Behav. 14:169-178.

Burger J, Gochfeld M. 1990. Nest site selection in least terns (*Sterna antillarum*) in New Jersey, New York (NY). Colon Waterbirds. 13:31-40.

Burger J, Gochfeld M. 1991. Experimental evidence for aggressive antipredator behavior in Black Skimmer (*Rynchops niger*). Aggress Behav. 18:241-248.

Burtner BF. 2011. Symbiosis between long-legged wading birds (Ciconiiformes) and Alligators (*Alligator mississippiensis*)? Testing the 'nest protector' hypothesis. [MSc thesis]. [Gainesville (Florida)]: University of Florida.

Burtner BF, Frederick PC. 2017. Attraction of nesting wading birds to Alligators (*Alligator mississippiensis*). Testing the 'nest protector' hypothesis. Wetlands. 37:697-704.

Castillo-Guerrero JA, González-Medina E, Fernández G. 2014. Seabird colonies of the small islands of Bahía Santa María-La Reforma, Sinaloa, México. Waterbirds. 37:439-445.

Clark PJ, Evans FC. 1954. Distance of nearest neighbor as a measure of spatial relationships in populations. Ecology. 35:445–453.

Clode D. 1993. Colonially breeding seabirds: predators or prey? Trends Ecol Evol. 8:336-338.

Clode D, Birks JD, Macdonald DW. 2000. The influence of risk and vulnerability on predator mobbing by terns (*Sterna* spp.) and gulls (*Larus* spp.). J Zool. 252:53-59.

Coulson J. 2002. Colonial breeding in seabirds. In: Schreiber EA, Burger J, editors. Biology of marine birds. Boca Raton (FL): CRC Press. p. 87-113.

Cueva HDL, Fernández G. 1996. Night feeding of Black Skimmers at Estero Tunta Banda, Baja California, Mexico. West Birds. 27:162-163.

Darling F, editor. 1938. Bird flocks and the breeding cycle. Cambridge (UK): Cambridge University Press.

Dinsmore SJ. 2008. Black Skimmer nest survival in Mississippi. Waterbirds. 31:24-29.

Emlen ST, Demong NJ. 1975. Adaptive significance of synchronized breeding in a colonial bird: a new hypothesis. Science. 188:1029-1031.

Erwin RM. 1977. Black Skimmer breeding ecology and behavior. Auk. 94:709-717.

Erwin RM. 1979. Species interactions in a mixed colony of Common Terns (*Sterna hirundo*) and Black Skimmers (*Rynchops niger*). Anim Behav. 27:1054-1062.

Fasola M, Canova L. 1991. Colony site selection by eight species of gulls and terns breeding in the "Valli di Comacchio" (Italy). Ital J Zool. 58:261-266.

Fuchs E. 1977. Predation and anti-predator behaviour in a mixed colony of terns *Sterna* sp. and Black-headed Gulls *Larus ridibundus* with special reference to the Sandwich Tern *Sterna sandvicensis*. Ornis Scand. 8:17-32.

Gochfeld M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. In: Burger J, Olla BL, Winn HE, editors. Behavior of marine animals. Vol. 7. New York (NY): Plenum Press. p. 207-270.

Götmark F, Andersson M. 1984. Colonial breeding reduces nest predation in the Common Gull (*Larus canus*). Anim Behav. 32:485-492.

Groom MJ. 1992. Sand-colored Nighthawks parasitize the antipredator behavior of three nesting bird species. Ecology. 73:785-793.

Gwynne J, Ridgely RS, editors. 2010. The birds of Brazil. The Pantanal and Cerrado of central Brazil. Ithaca (NY): Cornell University Press.

Hamilton WJ. 1971. Geometry for the selfish herd. J Theor Biol. 31:295-311.

Hatch JJ. 1970. Predation and piracy by gulls at a ternery in Maine. Auk. 87:244-254.

Hoogland JL, Sherman PW. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. Ecol Monogr. 46:33-58.

Junk WJ, Nunes da Cunha C, Wantzen KM, Petermann P, Strüssmann C, Marques MI, Adis J. 2006. Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. Aquatic Sci. 68:278-309.

Keller G. 1992. Nesting substrate preference and breeding success of Common Terns (*Sterna hirundo*) and Black Skimmers (*Rynchops niger*) on the Hampton Roads Bridge-Tunnel. [PhD thesis]. [Williamsburg (VA)]: The College of William and Mary.

Krannitz PG. 1989. Nesting biology of Black Skimmers, Large-Billed Terns, and Yellow-Billed Terns in Amazonian Brazil. J Field Ornithol. 60:216-223.

Krebs JR, Macroberts MH, Cullen J. 1972. Flocking and feeding in the Great Tit *Parus major* – an experimental study. Ibis. 114:507-530.

Kruuk H. 1964. Predators and anti-predator behaviour of the Black-headed Gull (*Larus ridibundus* L.). Behaviour Suppl. 11:3-7.

Lemmetyinen R. 1971. Nest defence behaviour of Common and Arctic Terns and its effects on the success achieved by predators. Ornis Fenn. 48:13-24.

Lima SL. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biol Rev. 84:485-513.

Lombard CD, Collazo JA, McNair DB. 2010. Nest and chick survival and colony-site dynamics of Least Terns in the U. S. Virgin Islands. Condor. 112:56-64.

Mariano-Jelicich R, Madrid E. 2014. Microsatellite variability among Black Skimmer (*Rynchops niger intercedens*) populations in southern South America. Waterbirds. 37:175-182.

Mariano-Jelicich R, Madrid E, Favero M. 2007. Sexual dimorphism and diet segregation in the Black Skimmer *Rynchops niger*. Ardea. 95:115-124.

Martin TE. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. Am Nat. 141:897-913.

Mayfield HF. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456-466.

Mellink E, Palacios E, Amador E. 2007. Colonies of four species of terns and the Black Skimmer in Western Mexico. Waterbirds. 30:358-366.

Nell LA, Frederick PC, Mazzotti FJ, Vliet KA, Brandt LA. 2016. Presence of breeding birds improves body condition for a crocodilian nest protector. PLoS One. 11(3): e0149572.

O'Connell TJ, Beck RA. 2003. Gull predation limits nesting success of terns and skimmers on the Virginia barrier islands. J Field Ornithol. 74:66–73.

Pius SM, Leberg PL. 1998. The protector species hypothesis: do Black Skimmers find refuge from predators in Gull-billed Tern colonies? Ethology. 104:273–284.

Quintana F, Yorio P. 1997. Breeding biology of Royal and Cayenne Terns at a mixed-species colony in Patagonia. Wilson Bull. 109:650-662.

Robert M, McNeil R, Leduc A. 1989. Conditions and significance of night feeding in shorebirds and other water birds in a tropical lagoon. Auk. 106:94–101.

Shealer DA, Burger J. 1992. Differential responses of tropical Roseate Terns to aerial intruders throughout the nesting cycle. Condor. 94:712–719.

Silva CD, Aguiar-Abdo MS, Oliveira DMM, Girard P. 2000. Caraterização ambiental do ninhal Corutuba, Pantanal de Barão de Melgaço, MT. In: Anais do III Simpósio sobre Recursos Naturais e Sócio-Econômicos do Pantanal. Corumbá (BRA): Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA-CPAP). p. 307.

Velarde E. 1999. Breeding biology of Heermann's Gulls on Isla Rasa, Gulf of California, Mexico. Auk. 116:513–519.

Vieira BP. 2017. Influence of environmental changes on the resource use and abundance of Black Skimmers. [PhD thesis]. [Glasgow (Scotland)]: University of Glasgow.

Whittam RM, Leonard ML. 2000. Characteristics of predators and offspring influence nest defense by Arctic and Common Terns. Condor. 102:301–306.

Yancey MR, Forys EA. 2010. Black Skimmers feed when light levels are low. Waterbirds. 33:556–559.

Zarza R, Cintra R, Anciaes M. 2013. Distribution, abundance and habitat selection by breeding Yellow-billed Terns (*Sternula superciliaris*), Large-billed Terns (*Phaetusa simplex*) and Black Skimmers (*Rynchops niger*) in the Brazilian Amazon. Waterbirds. 36:470–481.

Zusi RL, Garcia EFJ. 2017. Black Skimmer (*Rynchops niger*). In: Del Hoyo J, Elliott A, Sargatal J, Christie DA, Juana E, editors. Handbook of the birds of the world alive. Barcelona (ES): Lynx Edicions. Available from: http://www.hbw.com/node/54056