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ARTICLE

Incubation parameters, offspring growth, and behavioral adaptations to heat stress of Black Skimmers (*Rynchops niger*) in a Neotropical inland colony (Aves, Charadriiformes, Laridae)

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Abstract. This study focuses on incubation parameters, egg morphometrics, and body mass development, hatching, and behavioral adaptations to heat stress within a colony of freshwater-breeding Black Skimmers (*Rynchops niger*) located in the private nature reserve of Serviço Social do Comércio (SESC) in the northern Pantanal, Mato Grosso, Brazil. Temperatures of nest, eggs, and surface substratum, as well as the development of embryos, were surveyed using thermal imaging, a method allowing digital recording from a distance and in a fraction of the time of traditional measuring techniques. The mean egg dimensions ($n = 71$) were 4.48 (± 0.13) $\times$ 3.27 (± 0.07) cm; the mean mass at hatching was 24.3 (± 1.9) g, with a significant decrease over incubation time. The mean surface temperature of eggs varied from 30.9°C to 39.7°C, while the sand surface temperature was 20°C at 06:00 h, rising to 47.7°C at 11:00 h. There was a significant increase (7%) in egg surface temperature throughout incubation. Incubation-bout durations ($n = 2108$) were correlated with the microclimatic conditions of the substratum, becoming shorter with increasing sand-surface temperature around midday. Egg hatching lasted one day, and siblings hatched no more than 24 h apart. The mean body mass on Day 1 after hatching was 16.8 (± 1.6) g ($n = 6$). Three days after hatching, chicks moved to new sand depressions provided by parents near the original nest, where they remained motionless or tried to hide under riparian vegetation. The single chick that fledged had a growth rate of $K = 0.117$ and a t_{10-90} value of 37.3 days. On Day 7, dorsal pintail feathers and primaries appeared, which were open on Day 15. After 14 days, the chick was able to regulate its body temperature, and no more feeding by parental birds during the daytime was observed. On Day 21, the immature plumage was fully developed. Fledging was completed on Day 27. Our study demonstrates that thermal imaging is a useful method of surveying egg and embryo development in the Black Skimmer, reducing nest disturbance and observation efforts.

Keywords. Behavior; Embryonal development; Growth rate; Incubation; Thermal imaging.

INTRODUCTION

Black Skimmers (*Rynchops niger,* Rynchopidae) are tern-like waterbirds (40-50 cm, body mass c. 450 g) widely distributed in the Americas, including the Caribbean (Zusi, 1996; Zusi & Garcia, 2017). Within their southern range, skimmers often congregate in mixed colonies with terns (Laridae) in the reproduction period (Krannitz, 1989; Efe *et al.*, 2001; Zarza *et al.*, 2013; Antas *et al.*, 2016). Until recently, little has been known about the breeding of Neotropical freshwater colonies; a few studies have shed light on various aspects, such as the timing of reproduction, nest site selection and fidelity, behavior, survival rates, and predation (Zarza *et al.*, 2013; Antas *et al.*, 2016;

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Vieira, 2017; Schuchmann *et al.,* 2018). However, detailed information on chick development, temperature-regulation while brooding, and behavior, especially for the Neotropics south of the Amazon, is still full of gaps for Black Skimmers as well as for many other colonial breeders (see Schuchmann *et al.,* 2018).

The Pantanal of central South America is the largest natural freshwater system in the world and among the most important wetlands at a global scale (Alho *et al.,* 1988; Junk *et al.,* 2006), hosting an extremely diversified fauna and flora (Gwynne & Ridgely, 2010; Da Silva *et al.,* 2001). Successful adaptations to the extreme conditions between flood and dry seasons are crucial to the survival of both resident and migratory species (Junk *et al.,* 1989; Alho & Silva, 2012). With decreasing water levels, sandbanks and beaches along river margins become available for a few months as nesting grounds for many waterbirds, among them colonial seabirds (Raeder & Bernhard, 2003; Zarza *et al.,* 2013). Skimmer nests are formed of simple, shallow scrapes in such temporary sandbars, with neighboring nests often only being separated by a few meters or less (Zarza *et al.,* 2013; Antas *et al.,* 2016; Schuchmann *et al.,* 2018). In addition to predation as a serious threat to the nest survival of colonial ground-nesting seabirds (Antas *et al.,* 2016; Schuchmann *et al.,* 2018), the control and regulation of thermal conditions during incubation by parent birds are critical in maintaining relatively constant incubation temperatures in response to fluctuating daily ambient temperatures (Drent, 1975; Ward, 1990; Hart *et al.,* 2016). The reproductive phase of Black Skimmers in the Pantanal coincides with the dry season (c. June to October; Antas *et al.,* 2016; Vieira, 2017; Schuchmann *et al.,* 2018), when diurnal ambient temperatures frequently reach levels above 40°C (this study). Hence, behavioral and physiological strategies of skimmers are expected to reduce the impact of potentially lethal temperatures on clutches and offspring (Grant, 1982). To our knowledge, the detailed strategies adopted by breeding skimmers in response to heat stress are unknown.

Our study of a mixed-species colony of Black Skimmers with Large-billed (*Phaetusa simplex*) and Yellow-billed Terns (*Sternula superciliaris*) in the Brazilian Pantanal focused on the following major aims: (1) observation of hatching behavior, (2) analysis of ontogenetic development of chicks, (3) testing of thermal imaging as a feasible field method to estimate the embryo's development stages, and (4) providing data on incubation and chick behavior in response to environmental impacts, such as heat stress. We hypothesized that (1) an increase in ambient and/or sand-surface temperatures would reduce the incubation intervals and bout duration, and (2) the growth rate constant would be lower than that in temperate regions.

Since the study of nest and egg temperatures with traditional methods (constant thermosensor checks) might cause disturbances for incubating parent birds, a technique of distant thermal imaging was applied to examine nest microclimate parameters (McCafferty, 2013). The obvious advantage of this methodology is that measurements of the exact temperatures of eggs, chicks, and the immediate nest environment can be digitally screened from a distance and in a fraction of the time.

METHODS

Study site and observations

The breeding colony was situated in the northern Pantanal, within the private natural heritage reserve (RPPN) of Serviço Social do Comércio (SESC Pantanal) at Praia do Totelão (16°32′11.10″S, 56°23′58.20″W), an 11,502 m^2 (414 m long × 51 m wide) exposed sandbar along the Cuiabá River, 108 km southeast of the city of Cuiabá, Mato Grosso, Brazil (see Schuchmann *et al.,* 2018). As reported in a previous study of the same area (Antas *et al.,* 2016), we found *R. niger* associated with *Phaetusa simplex* and *Sternula superciliaris.* The colony was surveyed for 51 consecutive days from 10 August to 27 September 2015 (for details, see Schuchmann *et al.,* 2018). During the observation period, it consisted of two "subcolonies", one in the northern part (16°32′9.63″S, 56°23′57.26″W) and one in the southern part (16°32′12.46″S, 56°23′57.46″W) of the sandbar (Fig. 1). To reduce observer-induced disturbance, two camouflaged observation hides (Wildlife Photography Hide, Wildlife photography products) were placed c. 5-10 m away from the colony margins and repositioned according to specific observation demands during the reproduction period, *e.g.,* adult breeding behavior or chick activity. The two hides were established on the first day of the study period and were only moved within a small area to reduce disturbance or optimize the view of the nest sites. The first hide was set up in the northern breeding site and the second near the southern area.

Weather data

To analyze the impact of ambient factors on nesting parameters, we measured diurnal climatic variation during the study period by continuously (24/7) collecting weather data using a wireless weather station (Velleman WS1080) that was mounted c. 200 m away from the study site. Ambient temperature (°C) and relative humidity (%) were recorded at intervals of 30 minutes for 24 h per day (accuracy ± 0.1 min). The measured data were plotted from dawn until dusk at 30-min intervals (06:00-17:30 h). Due to a malfunction of the station, only data from 13 August onward could be used.

Nest sites and nest surveillance

At the beginning of observation (end of July), the study site was thoroughly inspected to register established nest sites. Surveyed *R. niger* nests were marked with colored flags for individual recognition and specifically coded (numerical and subcolony-related, *e.g.,*

Figure 1. Pantanal study site, Praia do Totelão (16°32′11.10″S, 56°23′58.20″W), an 11,502 m^2 (414 m long × 51 m wide) exposed sandbar along the Cuiabá River, 108 km southeast of the city of Cuiabá, Mato Grosso, Brazil. Numbers indicate Black Skimmer (*Rynchops niger*) nests (S and N), tents signify observation hides.

1N, 4S). Thereafter, regular inspections were performed every other day. New nests were considered to be active when there were one or more eggs inside the nest depression and visually confirmed by active incubation. Individual incubation times at each nest site and sex of adults were registered with each observed clutch-attending shift of parent birds (n = 2108). Nest site locations and their relation to the boundaries of the sandbank were marked and recorded by a GARMIN GPS 12 and GARMIN 78S, respectively, which enabled a reliable and accurate spatial assignment of each site within the limits of the measurement accuracy (± 3 m). The obtained geographical coordinates were transferred to a PC, and datasets were converted using the software DNR Garmin (version 5.4.1). The area of the study site was calculated with GEPath (version 1.4.5). Google Earth (version 7.1.5.1557) was used to illustrate and map nest site coordinates. We noted and documented all activities of parents and young. Observations were conducted by means of a spotting scope (KOWA PROMINAR TNS-3 with 77 mm objective lens and 40-60× optical zoom) and binoculars (Nikon Sporter Ex, 10 × 50). For video recordings of behavior, a camcorder (Panasonic HC-V550, 52× optical zoom) was used.

Eggs and growth rate parameters

The individual initiation of egg laying was recorded, and each egg was measured (length, width, mass) on the day of laying. Egg mass was weighed every second day until hatching to document changes throughout the incubation period. After hatching, chicks were color-marked (small ventral plumage color mark) for individual recognition. Prior of taking body measurements chicks were kept 2 min in cotton bags to calm down, while taking body mass data with a digital balance. Handling of chicks during data sampling of morphometrical features was with cloves; mensural handling of each chick took 5 min.

Growth rate parameters (*e.g.,* morphometric data, body mass) were taken every second day. Five mensural traits and body mass were taken: (1) bill length (distal point of the bill to the base of the bill, ± 0.01 mm); (2) bill width (at the base of the bill, ± 0.01 mm); (3) tarsus-metatarsus length (from the articulatio metatarsophalangis to the articulatio intertarsalis, ± 0.01 mm); (4) wing length (carpal joint to longest primary, ± 1 mm); (5) total length (distal point of the bill to the distal point of the tail, ± 1 mm); and (6) body mass, ± 0.1 g). Measurements were taken with a digital caliper (± 0.01 mm), a measuring tape (± 1 mm), and a digital balance (± 0.1 g). As a precaution, measurements and body mass data were taken in the early morning to minimize sun exposure on the chicks. These regular checks also provided a basis for estimating predation or lethal effects caused by diseases and/or nutrition deficits.

Thermal imaging

To survey the physical environment conditions of Black Skimmer clutches, egg temperature (T_e), nest temperature (T_n), and surface ground temperature (T_s) near the nests were monitored by thermal imaging. Thermal images were taken with a Fluke TI 100 camera (Fluke Corporation, USA), which has a thermal sensitivity (NETD) of ≤ 10°C at 30°C, a measurement range of -20°C to +250°C, and a spatial resolution (IFOV) of 3.39 mRad. The detector resolution was 160 × 120 pixels, and the minimum focus distance was 122 cm.

To record the thermal development stages of embryos until hatching and of nestlings, thermal images were taken at intervals of two days. The recordings were made at three different times per day: 06:00 h, 11:00 h and, depending on the observation times, at 14:00 h or 17:00 h. We also tested whether the eggs´ heat signature varied during the incubation period due to embryonal development.

Only nest sites with thermal images of more than three consecutive days were used for evaluation. For each image, the surface (eggs), nest (direct surroundings of the eggs), and environmental sand temperature (outside but near the nest boundary) were measured using Fluke SmartView® 3.

In addition to the thermal imaging of nests, sand temperature was measured with an infrared thermometer (digital IR-thermometer, WORKZONE), which enabled the measurement of surface temperature close to nest sites without disturbance. The instrument operates with a measurement time of 0.5 s and an accuracy of ± 1.5°C. Sand temperature was measured at intervals of 1 h during observation times.

Statistical analyses

To calculate the difference in incubation duration between male and female parents, linear mixed effects models (LMEs) were used with sex as a fixed factor. 'Nest ID' was added as a random factor to group the two sexes of each nest and to ensure their dependency. Additionally, a Wilcoxon rank sum test with continuity correction was conducted using the means. Duration was square-root-transformed to reduce the heterogeneity of variances.

To estimate the dependency of incubation duration on time of day, sand temperature, ambient temperature, egg temperature from day of laying, and location (subcolony), linear mixed effects models (LMEs) were used with each variable as a fixed factor. 'Nest ID' was added as a random factor to group the variables of each nest and to ensure their dependency. Data were considered significant when $p < 0.05$.

Statistical analyses were performed using R 3.2.2 (R Development Core Team, 2013) and the package *nlme* for calculating linear mixed effect models (Pinheiro *et al.,* 2012) and sciplot (Morales & R Development Core Team, 2012).

Growth rate and wing index

The growth rate constant (*K*) is proportional to the overall rate of nestling growth and allows direct comparisons, regardless of taxa, adult body mass or asymptote of the growth curve. Additionally, t_{10-90} is given as an inverse measure of growth rate expressing the time (days) required to grow 10-90% of the maximum body mass. This measure allows a comparison of nestling and incubation periods with the length of any other morphogenetic phase (Schuchmann, 1985).

Body mass data were analyzed with the following logistic equation:

$$W(t) = \frac{A}{(1 + e^{-K(t-t_i)})}$$

where W(t) is defined as body mass (g) at age t, A is the asymptote (g), *K* is the growth rate constant (days^{-1}), and t_i is age at the inflection point $(W = \frac{A}{2})$ (Ricklefs, 1967, 1973, 1976). Following (Ricklefs, 1967), t_{10-90} is an inverse measure of growth rate, related to *K* by the following equation:

$$t_{10-90} = \frac{4.4}{K_G}$$

The wing index of nestlings was calculated by dividing total body length (cm) by wing length (cm).

RESULTS

Weather data and sand temperature

The ambient temperature (T_a) decreased from 20.4°C at 06:30 h to 17.2°C at 12:30 h; from 13:00 h (19.7°C) until 17:30 h, it increased continuously to 32.8°C. The relative humidity showed an opposite trend. From 06:30 h to 12:30 h, the relative humidity increased from 72.5% to 76.2%, with small fluctuations of c. 3%. During the afternoon, it decreased from 70% (13:00 h) to 42.1% at 17:30 h.

The surface sand temperature (T_s) at 06:00 h was on average 17.3°C, increasing constantly throughout the morning up to a maximum of 45.6°C at 13:00 h. In the course of the afternoon, T_s decreased to 28.7°C at 17:00 h. Thus, the difference between the minimum temperature at sunrise and the maximum temperature at noon amounted to 28.3°C. The minimum T_s was 13°C (06:00 h), whereas the maximum T_s was 51.8°C (12:00 h); thus, adult Black Skimmers had to deal with a maximum temperature difference of 38.8°C.

Egg morphometrics and mass development

A total of 71 eggs (n = 29 clutches) of *R. niger* were registered, of which only 39 could be measured after laying due to predation by various egg robbers (Schuchmann *et al.,* 2018). The mean length was 4.48 (± 0.13) cm, the mean width was 3.27 (± 0.07) cm, and the mean mass was 24.3 (± 1.9) g. Only three nests (n = 7 eggs) were surveyed until hatching; there was a significant loss in egg mass throughout the incubation period (Fig. 2). Egg masses between individual nests differed considerably. For example, the maximum egg mass on the first day of incubation was 27 g (nest 4S), while the minimum mass was 22.2 g (nest 2S); at the end of the incubation period, these eggs weighed 23.2 g and 20.8 g, respectively. A difference of c. 3-4 g from the other two clutches persisted during the whole incubation period.

Hatching, behavior of offspring, and nest survival

In general, the hatching procedure lasted one day. Parent birds provided some physical support during the progress of eggshell freeing by brief incubation-position changes. Each sibling hatched with a time difference of 24 h. After hatching was completed, the parent birds disposed of the eggshells by taking them out of the nest, sometimes by flying but mostly by walking a few meters away from the nest site (~2-5 m).

Twenty-four hours after hatching, the precocial nestlings left the nest for short distances (~50 cm) and started begging behavior. On Day 3, offspring moved to new shallow sand depressions provided by the adults, c. 2-3 m away from their original nest. Independent of location (*i.e.,* with or without some protection by vegetation, etc.), the chicks remained there, mainly shadowed by their parents.

Of the total number of 15 hatched young (6 nests), only 6 survived the first 5 days (5 days: 3; 6 days: 1; 7 days: 1), and only a single chick fledged successfully. All other chicks died, mostly due to predation, resulting in an overall fledging success of only 3% (for details, see Schuchmann *et al.,* 2018).

Variation in egg, nest, and surface temperature

A total of 338 thermal images of clutches were obtained throughout the study period, initially with 25 eggs from 9 different clutches recorded and analyzed. However, due to predation or nest abandonment (Schuchmann *et al.,* 2018), chicks hatched from only seven eggs. The diurnal variations in the mean temperature of eggs (T_e), nests (T_n), and sand surfaces (T_s) are presented in Table 1. All three variables were lowest at 06:00 h and highest between late morning and mid-afternoon. T_s showed the highest fluctuation (mean average Δ 27.7°), while fluctuation was much lower in T_e (8.8°). A marked difference of 7°C between T_e and T_n was registered at 06:00 h, although both varied in an almost equal range.

Figure 3 illustrates differences in nest, egg, and ambient temperatures in early (3A) and late morning (3B) based on thermal imaging. The mean nest and egg temperatures were more than 5°C above the ambient substratum at approximately 06:00 h. The opposite scenario occurred around noon, when sun heated the sand surface

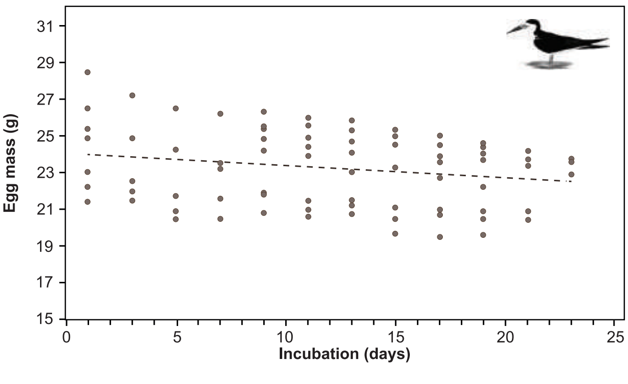

Figure 2. Egg mass development in three surveyed Black Skimmer (*Rynchops niger*) nests (n = 7 eggs, 84 measurements) until hatching at Praia do Totelão, Pantanal, Mato Grosso, Brazil, throughout the incubation period in July-September 2015. Note that the number of eggs decreased to three toward the end of incubation due to predation. The regression line indicates a negative trend ($R^2 = 0.043$, $p < 0.05$, LME) of egg mass over incubation time.

to > 50°C, while the temperatures of nest cup and eggs were more than 10°C lower. The eggs were surrounded and/or covered by water drops (indicated by bluish spots) that were delivered frequently by parents through belly soaking (*i.e.,* wetting of the ventral plumage).

Variation in egg temperature development

Figure 4 shows egg temperatures (T_e) during the ongoing incubation period. We recorded a clear variation in T_e, revealing a significant increase of approximately 7% from Day 1 to hatching date (LME: $R^2 = -0.837$, $t_{1,328} = -8.017$, $p = 0.0138$). The overall mean T_e during incubation was 35.8 ± 4.5°C.

Developmental stages of the embryo

To test the feasibility of using thermal imaging to determine the developmental stages of *R. niger* embryos in the field, thermal images of one nest (4S) were juxtaposed with related photographic images in three different stages of the incubation progress (Fig. 5). At Day 8, eggs still showed a uniform heat signature (yellow, Fig. 5A), whereas on Day 14, the heat signature indicated air cells inside two of the eggs (Fig. 5B). Two days before the hatching of the first egg (Day 18), air cells were enlarged (Fig. 5C) and visible in all eggs. The heat signature also revealed the approximate location and shape of the embryos inside the egg.

Table 1. Diurnal variation (± standard deviation, n = 338 measurements) of the mean temperature of eggs (T_e) (n = 25) and nests (T_n) (n = 9) of the Black Skimmer (*Rynchops niger*) and sand surface temperature (T_s) at Praia do Totelão, Pantanal, Mato Grosso, Brazil, from July to September 2015.

		Temperatures (total)					
Time	**n**	**T_e (°C)**	**± SD**	**T_n (°C)**	**± SD**	**T_s (°C)**	**± SD**
06:00	110	30.9	3.9	23.9	1.8	20.0	1.8
11:00	105	39.7	1.4	37.4	3.3	47.7	4.0
14:00	43	38.9	1.4	36.5	2.9	42.7	7.6
17:00	80	35.8	1.6	31.8	1.7	29.1	2.0
Range (°C)		19.8 – 43.2		19.0 – 43.3		14.9 – 55.4	

Incubation duration

We tested the dependence of incubation duration on sex, time of day, and ambient temperature. During the diurnal phase, adult skimmers were incubating constantly. The pairs (n = 25) alternated frequently, with one partner incubating and the other resting on the sandbank. The overall mean incubation-bout duration was 20.6 ± 15.65 min (n = 2108). There was no significant difference in bout duration between the two subcolonies (LME: $R^2 = -0.613$, $t_{1,22} = 1.612$, $p = 0.1212$), but bout duration differed significantly between sexes. Female bouts were on average 22.96 ± 16.39 min, while those of males were shorter at 18.04 ± 14.32 min (LME: $R^2 = -0.284$, $t_{1,2065} = -8.554$, $p < 0.01$, Mann-Whitney U test).

Regarding diurnal effects, there was an overall significant decrease in incubation time during the day (Fig. 6). The mean duration of the incubation bout

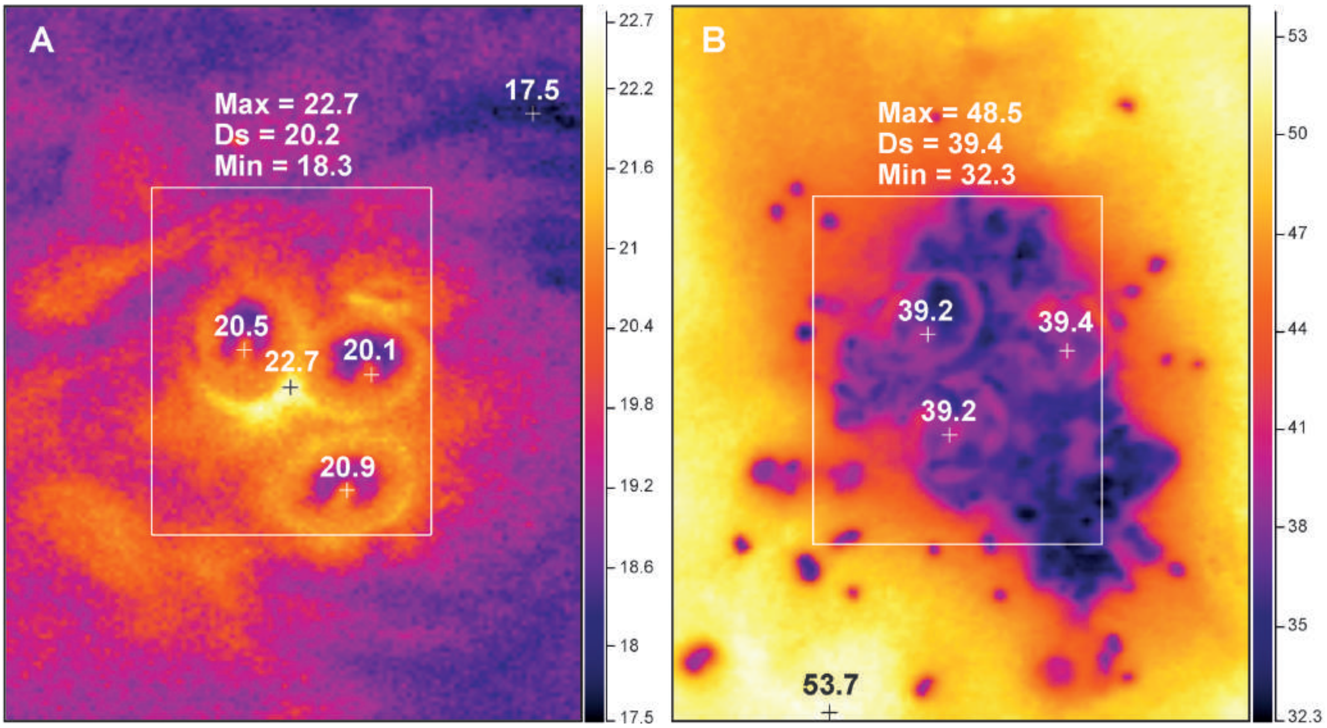

Figure 3. Thermal images of a Black Skimmer (*Rynchops niger*) nest (12N, white rectangles) at Praia do Totelão, Pantanal, Mato Grosso, Brazil, taken on the same day (6 September 2015) in the early (05:59 h, A) and late morning (11.45 h, B), showing the mean (Ds), minimum, and maximum nest temperature, surface ground temperature (crosses), and egg surface temperature (within rectangles). Scale on right: color scale associated with the respective temperatures. With a special optical filter water drops were visualized (Blue and red circles outside the nest and next to the three clutch contours) which were taken to the nest by both adults. Note in Fig. B the sand surface temperature of 53.7°C. Photos by CO.BRA/INAU.

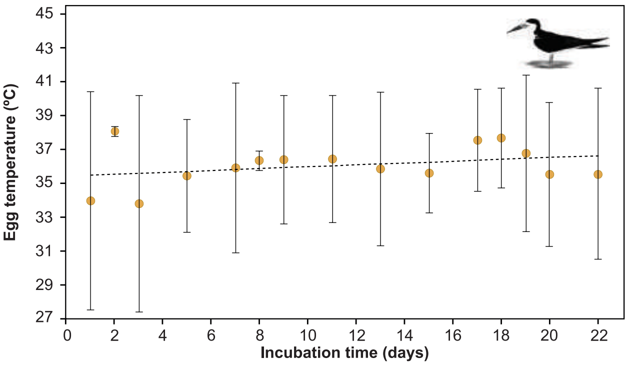

Figure 4. Mean surface temperatures (T_e) of 25 eggs (n = 7 nests) of the Black Skimmer (*Rynchops niger*) at Praia do Totelão, Pantanal, Mato Grosso, Brazil, during incubation from July to September 2015; not all eggs reached hatching. Confidence intervals are indicated by bars; the regression line (dotted) represents a significant increase between Day 1 and hatching ($R^2 = 0.098$, $p < 0.01$, LME).

at 06:00 h was 42.3 ± 24.1 min. During late morning (11:00 h), the mean bout duration increased slightly to 23.5 ± 16.6 min, in contrast to 16.9 ± 9.9 min at 10:00 h. The minimum bout duration was 8.6 ± 7.2 min in late afternoon (16:30 h).

The impact of temperature variables is shown in Fig. 7. Incubation activity was greater at temperatures from < 20°C to 25°C (Fig. 7A) and slightly less at 30°C to 35°C. However, LME yielded no significant impact on incubation duration ($p = 0.721$). On the other hand, an increase in ground-surface (sand) temperature (Fig. 7B) had a negative impact on incubation duration.

Hatching and behavior of chicks

The hatching procedure lasted one day. Parent birds provided some physical support during the progress of eggshell freeing by incubation position changes at short intervals. Siblings hatched with a time difference of 24 h. After hatching was completed, the parent birds disposed of the eggshells by taking them out of the nest, sometimes by flying but mostly by walking a few meters away from the nest site (c. 2-5 m). Twenty-four hours after hatching, the precocial nestlings left the nest for short distances (c. 50 cm), showing begging behavior toward the parent birds. On Day 3 after hatching, chicks moved to new shallow sand depressions provided by the adults c. 2-3 m away from their original nest. Independent of location, the chicks remained there, mainly shadowed by their parents. Of a total number of 15 hatchlings (6 nests), only 6 survived the first three days (five days: 3; six days: 1; seven days: 1; fledged: 1). All other chicks died, mostly due to predation (for details, see Schuchmann *et al.,* 2018).

Body mass development and growth rate

Hatchlings (n = 6) had a mean body mass of 16.8 ± 1.6 g on Day 1, a difference of 6.6 g from the average egg mass before hatching (23.4 ± 0.36 g). While hatchlings weighed 26.1 g (± 3.2) at Day 3, they almost doubled their body mass by Day 5 (43.6 ± 9.9 g). The lowest body mass at hatching was 14.3 g (chick R1-2); from Day 3 to Day 5, and the body mass of this hatchling decreased from 18.1 g to 14.9 g. Its sibling (R1-1) hatched with a body mass of 15.4 g, almost doubling its body mass between Day 3 and Day 5 to the highest found (59.2 g). Two siblings in nest 1N showed a different development pattern. The hatching weight of the siblings differed by only one gram (1N-1 = 17.7 g; 1N-2 = 18.7 g), but the body mass of 1N-1 increased much faster to 29.3 (vs. 20.4) g on Day 3 and to 41.9 (vs. 31.3) g on Day 5.

The body mass of the only chick to successfully fledge (R1-1) was 15.4 g at hatching (Day 1) and 59.2 g on Day 5. A strong increase was observed from Day 9 (99.3 g) to Day 11 (142.4 g), an increase of 43.4%. The maximum value was observed on Day 21 at 208.8 g, decreasing until Day 25 (182.2 g) two days before fledging (the last measured value). The growth rate constant (*K*) for this chick was 0.117, and the t_{10-90} value was 37.7 days.

Morphometric parameters

Measurements of mensural traits (bill length – BL, bill width – BW, tarsus length – TS, total body length – TL, wing length – WL) of the single chick reaching the fledging phase (R1-1) are shown in Fig. 8. On the day of hatching, BL was 94 mm, BW was 72 mm, and TS (95 mm) was almost equal to BL (Fig. 8A). Considering the gradients of BL and TS, the growth of these two parameters was similar until Day 14. Thereafter, BL increased faster (411 mm at fledging) than TS (307 mm at fledging). BW increased more slowly than the other two parameters, reaching 164 mm at fledging.

Comparison of total length and wing length (Fig. 8B) revealed that during the first 7 days, TL progressed more rapidly than WL. TL at hatching was 720 mm, with a WL of 160 mm. From Day 9 on, both gradients developed almost parallel to each other. At fledging, WL was 210 mm, and TL was 297 mm.

The correlation between TL and WL is expressed as the wing index (WI). The rapid growth of the chick was reflected by an increase in WI from 4.4 at hatching date to 6.0 on Day 3, after which the WI decreased to 1.4 two days before the appearance of pinfeathers, with the highest difference between Day 7 (WI = 4.3) and Day 9 (WI = 3.0).

Plumage development

Chicks of *R. niger* exhibit characteristic camouflaged down plumage (Fig. 9A-C). On Day 7, body pinfeathers appeared dorsally, and primaries developed on the wings (Fig. 9B). On Day 15, the primaries were open (Fig. 9D). The down plumage disappeared on Day 21, and the immature plumage was completely developed (Fig. 9E).

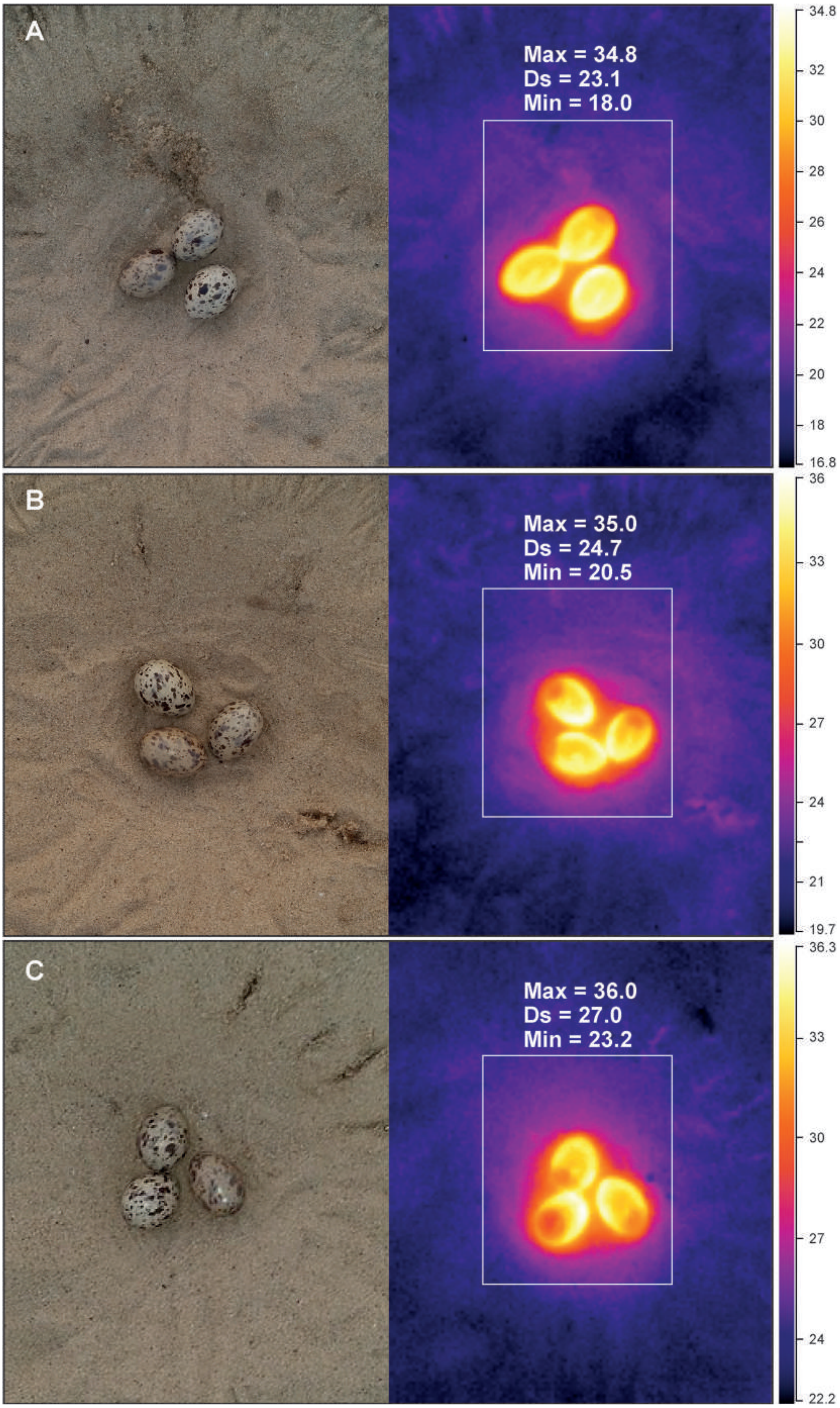

Figure 5. Developmental stages of a Black Skimmer (*Rynchops niger*) clutch (nest 4S) at Praia do Totelão, Pantanal, Mato Grosso, Brazil, from July to September 2015, with three fertilized eggs revealed by thermal imaging (right); with maximum (Max), minimum (Min), and mean temperature (Ds) inside the nest (white outline). Stages: (A) Day 8, (B) Day 14, and (C) Day 18 (two days before hatching). Note the well-camouflaged eggs inside the nest depression exhibiting some variation in shell pattern (left), with narrow corrugations caused by adults' bills when relocating the eggs. Photos by CO. BRA/INAU.

Activity behavior of young

During the first five days of life, chicks were entirely cared for by the parents before they became partially autonomous; in the early morning and in the evening, no parental care was observed. In the absence of parental birds, juveniles hid under the scarce riparian vegetation or remained in a shallow sand scrape without any movement.

The single juvenile that successfully fledged was able to completely regulate its body temperature 14 days after hatching, having then reached a body mass of 169.8 g. Afterward, during daytime, no more brooding or feeding attempts by adults were observed. The chick remained close (≤ 1 m) to the river shoreline. During most of the growth phase, the chick showed no aggressive or defensive behavior toward researchers and remained silent in its shallow scrapes rather than running away. However, on Day 25, two days before fledging, the first defense behavior was observed during measurements (*e.g.,* pecking at fingers, screaming). On Day 27, fledging was completed. Afterward, the juvenile was still observed on the sandbank, sometimes flying in a flock together with adults. Most of the time, it remained resting close to the riparian area, rarely accompanied by adults, and foraging attempts or feeding by parent birds were not observed during the day.

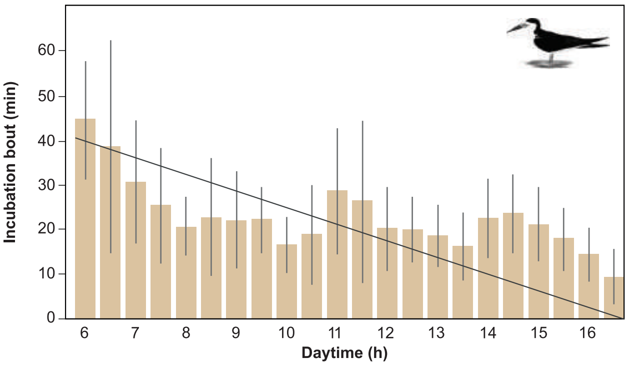

Figure 6. Incubation-bout duration of Black Skimmers (*Rynchops niger*) (n = 9 nests) at Praia do Totelão, Pantanal, Mato Grosso, Brazil, from July to September 2015 in relation to time of day. Lines indicate standard deviation (SD); LME: $R^2 = -0.778$, $t_{1,2082} = -8.017$, $p < 0.001$.

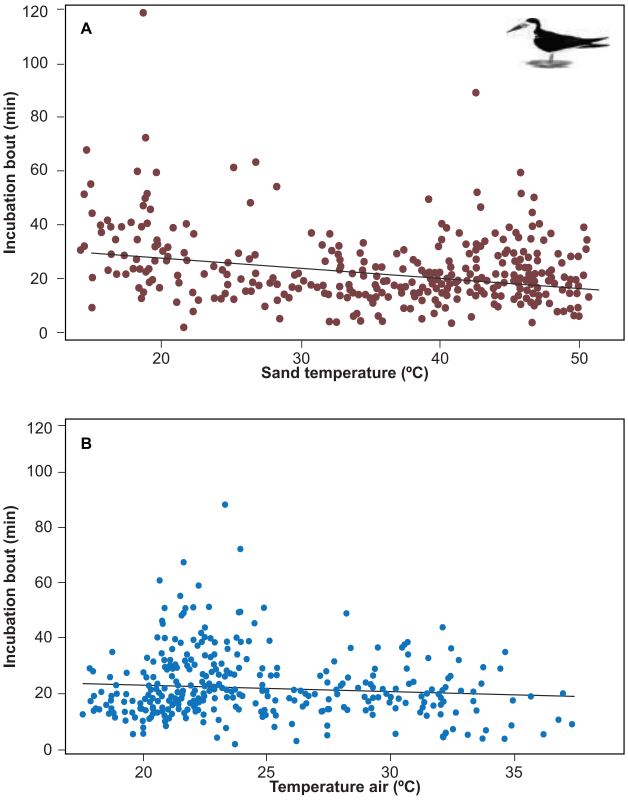

Figure 7. Incubation-bout duration (min) of Black Skimmers (*Rynchops niger*) (n = 9 nests) at Praia do Totelão, Pantanal, Mato Grosso, Brazil, from July to September 2015 in relation to mean ambient temperature (A) and ground-surface temperature (B). Regression shows no correlation with ambient temperature (A) $R^2 = -0.88$, $t_{1,1557} = -0.357$, $p = 0.721$, LME) but a significant decrease during higher surface temperatures (B) $R^2 = -0.731$, $t_{1,1969} = -7.969$, $p < 0.001$, LME).

DISCUSSION

Nests are known to play multiple roles in the control of the microclimatic parameters for egg and offspring development (Deeming & Ferguson, 1991; Deeming, 2002; Hart *et al.,* 2016). In the case of ground-nesting tropical birds that do not build sheltered nest cups, specific breeding strategies are needed to counteract thermal fluctuations (*i.e.,* warming) of nests and eggs by the

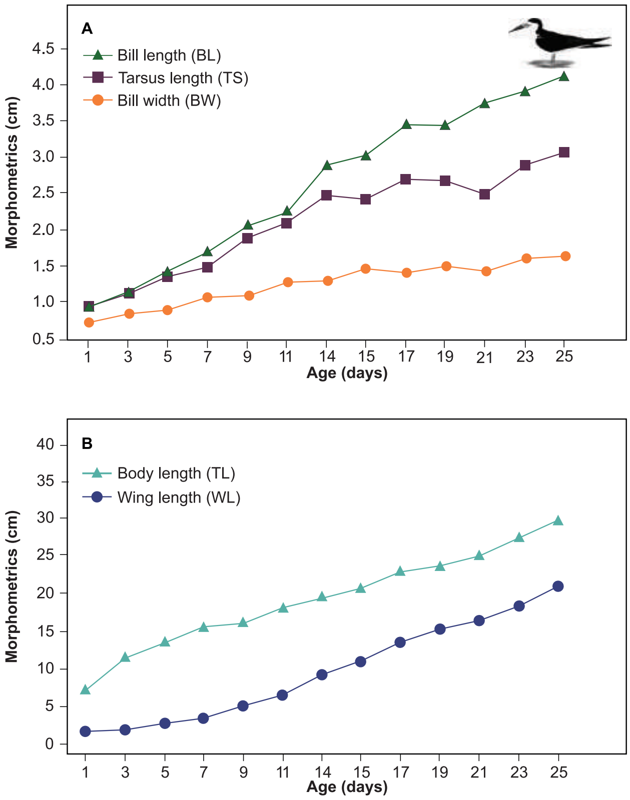

Figure 8. Mensural data of the single Black Skimmer (*Rynchops niger*) chick surveyed in August-September 2015 that reached the fledging phase at Praia do Totelão, Pantanal, Mato Grosso, Brazil (n = 1; accuracy = ± 0.01 cm). (A) Development of bill length (BL), bill width (BW), and tarsus length (TS) as a function of age (days). (B) Development of total body length (TL) and wing length (WL) as a function of age (days).

substratum and ambient temperatures influenced by solar radiation (Hart *et al.,* 2016). The optimal incubation temperature for wildfowl eggs ranges between 33°C and 39°C (Nakage *et al.,* 2003). Previous data for Black Skimmers (Grant *et al.,* 1984: 35.1°C ± 0.6°C; Deeming & Ferguson, 1991: 35.1°C) are similar to our results (mean T_e = 35.8°C ± 4.5°C). T_n was lower than T_e at all times, which could be because the nest substrate often consisted of wet sand leading to an evaporative cooling effect. Many avian eggs undergo significant increases in T_e as incubation proceeds (Deeming & Ferguson, 1991). For instance, in the eggs of Herring Gulls (*Larus argentatus*), the mean T_e increased by 7°C from the beginning to the end of incubation (Drent, 1970). Likewise, our data

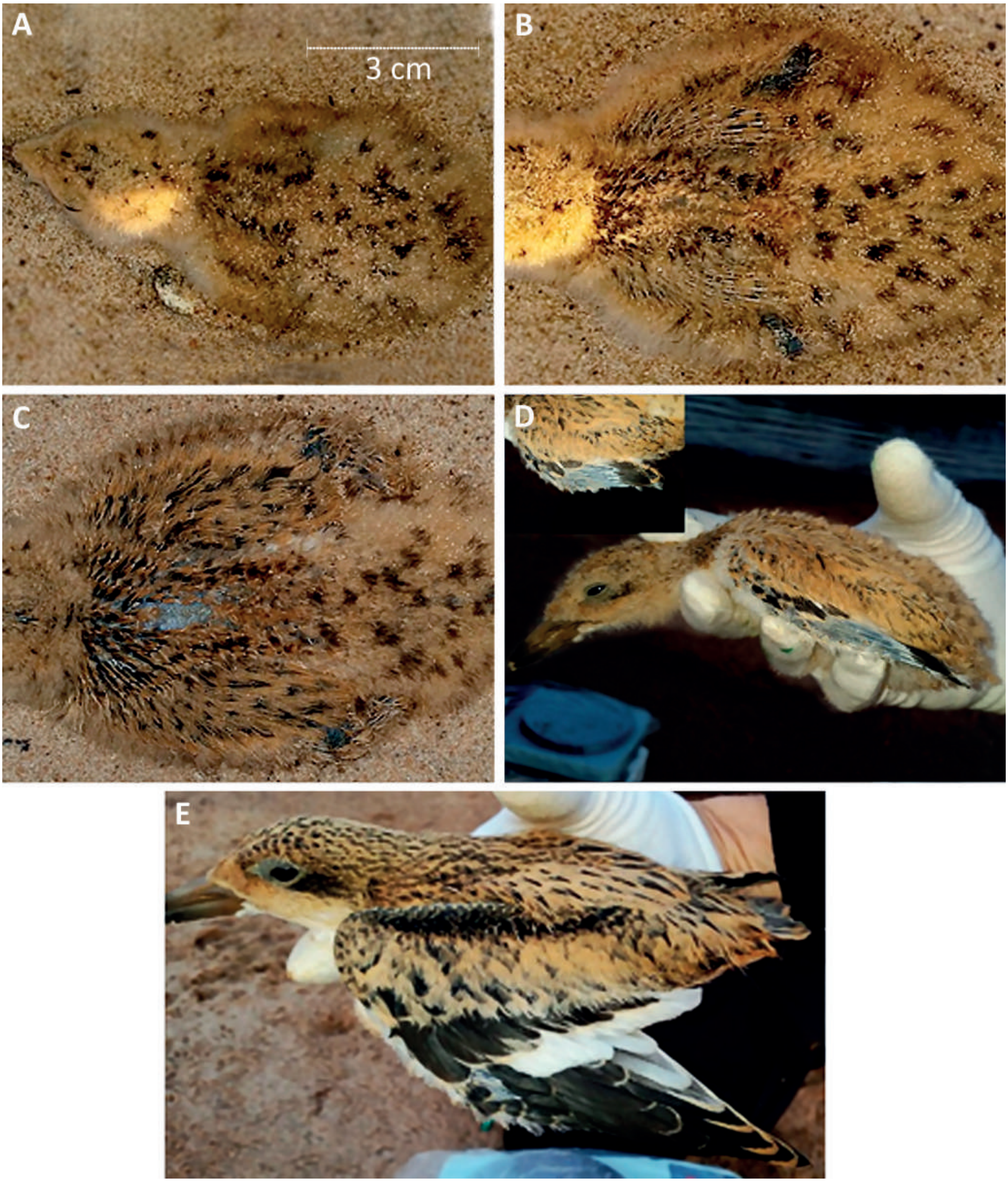

Figure 9. Plumage development of a Black Skimmer (*Rynchops niger*) chick from Praia do Totelão, Pantanal, Mato Grosso, Brazil. (A) Camouflaged down plumage (Day 3); (B) appearance of dorsal pinfeathers and primaries (Day 7); (C) dorsal pinfeathers opened (Day 11); (D) primaries opened (Day 15); (E) completely developed immature plumage (Day 21). Photos: CO. BRA/INAU.

showed that the mean T_e of Black Skimmer eggs significantly increased (by c. 7%) during the incubation period.

Adult ground-nesting birds may respond to a critical increase in egg temperatures by frequent intervals between incubation bouts. For example, incubation duration in Kentish Plovers (*Charadrius alexandrinus*) is directly correlated with ambient temperature (Amat & Masero, 2006; Amat *et al.,* 2012). In the present study, substratum temperature was positively correlated with the frequency of incubation bouts, supporting our working hypothesis. However, egg temperature (T_e) and nest temperature (T_n) varied over a wide range (between c. 20°C and 43°C) during the diurnal phase, with the maximum T_e reaching even a lethal limit in one nest (6S) over an extended period of time (Webb, 1987). However, as these particular eggs still hatched, the period of time between adult switching or disturbance, and thus egg exposure to the sun, was obviously short enough to maintain normal embryo development, as has been observed for attended nests of Sooty Terns (*Onychopryon fuscatus*) (Howell & Bartholomew, 1962). The slight increase in the mean break duration between 11:00 h and 12:00 h in our study may indicate that the adults extended incubation breaks by bathing to reduce their own body temperature during the hottest time of the day.

Wetting of the ventral plumage in parental birds, so-called belly soaking, is another strategy to cool down eggs or to supply chicks with water and is found in species breeding in dry steppe, desert, or sandy areas, *e.g.,* sandgrouse (*Pterocles* spp., Cade & Mclean, 1967), plovers (*Charadrius* spp., Mclean, 1974), terns including Common (*Sterna hirundo*), Sandwich (*S. sandvicensis*), and Royal Tern (*Thalasseus maximus*) (Grant, 1981; Nisbet, 1983), as well as in the closely related African Skimmer (*R. flavirostris,* Roberts, 1976). Such behavior is also known from New World skimmers (Zusi, 1996) and observed in our study. However, belly soaking may also serve as a thermoregulation measure in adult birds (Amat *et al.,* 2012).

For the first time in a field study, the current work applied thermal imaging to record egg temperatures (McCafferty, 2013) and the developmental stages of Black Skimmer clutches. In addition to providing temperature data, our results confirmed that thermal imaging enables valuable insights into embryonic development. During the first days after egg laying, the heat signature of skimmer eggs was evenly distributed, as indicated by the uniform spatial patchiness of the egg yolk at the very beginning of the embryo (Fig. 5A). With ongoing development, the broad end accommodates the air cell (Fig. 5B), and the shell surface overlying the cell shows a greater pore density than the remainder for an improved gas exchange (Deeming & Ferguson, 1991). Finally, air cells grow in the course of incubation because of water vapor loss (Paganelli *et al.,* 1974; Fig. 5C).

Regarding morphometrics, in North Carolina (USA), egg length in Black Skimmers was 4.67 ± 0.04 cm, and the width was 3.34 ± 0.03 cm (Grant *et al.,* 1984). For a broader region in the Pantanal, including our study site (Antas *et al.,* 2016), the mean egg dimensions were 4.37 ± 0.24 cm and 3.26 ± 0.13 cm, respectively, both of which are very close to our findings. Similarly, the mean egg mass (24.3 ± 1.9 g) was similar to that of the other study in the Pantanal (Antas *et al.,* 2016: 23.3 ± 2.5 g) but c. 15% lower than the mean egg mass recorded for the Atlantic colony (28.51 ± 0.49 g) (Grant *et al.,* 1984). However, the egg mass decrease in North Carolina (11.6%) was similar to our data and was likely caused by fractional water loss (Grant *et al.,* 1984). Overall, fluctuations in average egg mass yielded by our three measured nests were relatively small (< 1 g). The fact that the egg mass in one nest was markedly lower could be explained either by being a second clutch or by age/condition, since experienced females in birds tend to reproduce better (*i.e.,* higher egg mass) due to their enhanced prolactin and corticosterone levels (Riechert *et al.,* 2012). The inflection points at Days 5 and 7 could be related to a combination of water vapor loss (Paganelli *et al.,* 1974) and embryonal development.

The growth rate constant at Praia de Totelão was c. 30% lower than reported in previous studies from Virginia, USA (Erwin, 1977: K = 0.228; Gordon *et al.,* 2000: K = 0.18), and in several tern species (Ricklefs, 1968). Thus, our data support the hypothesis that tropical taxa grow more slowly (here, c. 25% less) than taxa from temperate regions (Ricklefs, 1968, 1976). The single fledgling had a lower body mass than chicks from Virginia (Erwin, 1977: males/females 264.4/295.2 g; Gordon *et al.,* 2000: 243 g), but we hesitate to interpret this result in view of the sample size and different weighing methods. Differences may also be geographically related, since there is considerable variation in the body mass of adult skimmers from different breeding grounds (Scherer *et al.,* 2013: 199-394 g). Due to the dominance of the first-hatched chick and rivalry for food, siblings show different growth rates (Zusi, 1996).

Skimmer chicks usually leave the nest after the first day after hatching (this study). In *R. niger,* they are guided to new nest depressions by parents (Schuchmann *et al.,* 2018) before they become active themselves. Young *R. flavirostris* started to wander around their breeding islets (Roberts, 1976). In both species, the well-camouflaged chicks (cf. Fig. 9) try to hide from predators (*i.e.,* gulls, birds of prey, caimans) in the absence of parents by adressing to the ground or hiding in sparse riverine vegetation (Roberts, 1976; Schuchmann *et al.,* 2018). We did not record any instance of chicks being transported by parents by picking them up in the case of potential threats, as has been observed for *R. flavirostris* (Roberts, 1976).

CONCLUSIONS

Parental responses to heat stress in ground-nesting seabirds, such as *R. niger,* comprise diverse behavioral strategies to successfully maintain the development of eggs or embryos. Active control of nests could explain the abandonment of clutches even without detectable causes (Schuchmann *et al.,* 2018), indicating that parental birds may be aware of the current status of eggs or embryos and may quit them in the case of irregularities. Since reliable breeding data, even in many widely distributed Neotropical species, are scarce (Cordoba-Cordoba *et al.,* 2010), further investigations, especially from understudied regions such as the Pantanal (Antas *et al.,* 2016), are strongly recommended. Such investigations are important to document adaptations in breeding caused by the impact of environmental stress factors over time, such as climate, water-level changes, and nest site disturbance (Matthysen *et al.,* 2011).

Outlook

Due to ongoing economic pressure (Junk *et al.,* 2006; Alho, 2008), the Pantanal is perhaps the most prominent example of human-induced changes (*i.e.,* by deforestation, farming, water extraction) in a large Neotropical freshwater wetland, causing long-term impacts on the landscape topography and biodiversity of this enigmatic region (Alho, 2011; Alho *et al.,* 1988). Its fine-tuned and complex ecological balance through a flood-pulse system (Junk *et al.,* 1989) is not only important in maintaining species richness and seasonal turnover but also, and perhaps even more importantly, has a priceless value for ecosystem services (Seidl & Moraes, 2000). The future survival and composition of fauna and flora, including behavioral adaptations such as avian breeding strategies, will depend on how massive the future impact of water extraction by giant hydroelectric dams currently installed around the Pantanal will be (Crabb *et al.,* 2017).

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