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Nesting behaviour of Black Skimmers (*Rynchops niger*) along the Manu River, Peru

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Abstract

The Black Skimmer (*Rynchops niger*) nests on the river beaches in the Amazon region during the dry season, where there a lack of studies on its habitat selection and behaviour during nesting. The species exhibits biparental care and sexual size dimorphism, where the male is larger. Firstly, the study aimed to contribute to knowledge on habitat and nest-site selection of Black Skimmers in Amazonia. Secondly, to determine whether nests and incubating adults were affected by high temperatures, and if so, how the species adjusts its behaviour. Thirdly, to observe diel incubation patterns and its relation to sexual conflict between males and females. Data were collected during one breeding season on a section of the Manu River in the Peruvian Amazon.

Wider beaches were favoured by Black Skimmers, on which nests were usually placed close to the river and further away from the vegetation. Large temperature fluctuations were recorded on the beach surfaces, while nest temperature was comparatively constant. Black Skimmers shortened incubation bouts with higher temperature and performed thermoregulatory behaviours at the nest. Both males and females contributed, but females incubated slightly more and sat for longer bouts on the nest.

Nest site selection of Black Skimmers seems to favour reduced predation risk away from shading vegetation. As a consequence, potential for overheating of both eggs and incubating adults was high. However, the biparental system allowed for almost constant incubation, protecting the nest from adverse temperatures. Although the species seems to be adapted to incubation in a thermally stressful nesting environment, further studies are needed to reveal the thermal tolerances of Neotropical open ground nesting birds, particularly in light of predicted temperature rise in the region.

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1. Introduction

The complexity of floodplain habitat in Amazonia is driven by intensity and frequency of flooding, river erosion and deposition as well as different nutrient contents between rivers (Cintra et al. 2007; Remsen & Parker 1983; Robinson & Terborgh 1997). Open beaches on river banks are the first habitat type in a primary succession process towards mature floodplain forest, kept relatively free from permanent vegetation by regular flooding (Remsen & Parker 1983; Terborgh 1985). Variation in river level makes this habitat highly dynamic, with the extent of beaches varying between years and within seasons (Raeder & Bernhard 2003, Zarza et al. 2013). Bird species breeding on these beaches are few (Terborgh 1985), but their nesting is highly dependent on river levels which decrease during the dry season and expose the beaches (Groom 1992; Zarza et al. 2013). The close link between floodplain avifauna to seasonal flooding of rivers, make this community vulnerable to alterations in river flow (Remsen and Parker 1983). Climate change and direct anthropogenic influence such as dam construction are affecting Amazonia’s rivers (Junk 2013), highlighting the need for further knowledge on birds nesting along these rivers.

Understanding the distribution across habitats has been recognised as important for species conservation efforts (Heinanen et al. 2008; Jones 2001; Jonzén 2008). Different habitats offer varying fitness prospects, and therefore the choice of habitat by birds could be acted upon by natural selection (Chalfoun & Schmidt 2012). This should lead to specific preferences by species, particularly for nesting habitat due to its large consequences on fitness (Clark & Shutler 1999). Nevertheless, Hildén (1965) points out that there might be a treshold between settling and continuing to search for new areas, resulting in birds not always selecting optimal sites. A habitat can also function as a a sink, where a population is sustained by by dispersers from more productive areas, and not from reproduction within the population (Jonzén 2008; Pulliam 1988). Further, habitats can function as ecological traps, where individuals in a population disproportionally select inferior quality habitat although better habitat exists, due to misinterpretations of environmental cues (Battin 2004). Additionally, human induced changes can restrict the use of optimal habitat or influence the cues used in habitat selection (Chalfoun and Schmidt 2012; Heinanen et al. 2008; Jonzén 2008). Thus, due to the possible use of non-optimal habitat, solely observing presence of nesting birds may not be sufficient without understanding habitat effects on reproductive behaviour and outcome (Jones 2001).

The negative effects on egg hatching and offspring phenotype, induced by slight temperature deviation from the optimum, should put birds under selection pressure to prefer nest sites where they are able to maintain suitable nest temperature (DuRant et al. 2013; Mainwaring 2015). It has been shown that predation reduction and microclimate can be optimal in different sites, leading to a trade-off in nest site selection and thus avoidance of shading structures associated with predation (Amat & Masero 2004a; Tieleman et al. 2008). An additional trade-off has been suggested for Amazonian beach nesting birds, which often select sites close to the river at the expense of higher flood risk, possibly to benefit from potentially cooler sand substrates for nests (Davenport et al. 2016; Groom 2013).

Contact incubation, where the bird sits in contact with the eggs, is in most bird species essential for maintaining appropriate nest microclimate (Deeming 2002). However, it restricts the incubating bird to the nest, during which it can be exposed to predation and the physical environment (Alrashidi et al. 2010; Deeming 2002). In periods of high temperatures, the incubating bird might have to resort to mechanisms of evaporative cooling to be able to stay on the nest (Bartholomew & Dawson 1979; Walsberg & Voss-Roberts 1983). Nevertheless, some self-maintenance activities cannot be carried out at the nest (Deeming 2002), and birds might need to trade-off nest attendance with cooling mechanisms carried out away from the nest (Amat & Masero 2004b). In biparental incubation, one of the parents can relieve the other at the nest, presumed to decrease the conflict between incubation and self-maintenance activities in comparison to uniparental incubation (Alrashidi et al. 2010; Bulla et al. 2015; DuRant et al. 2013). Thus, biparental incubation may be essential for breeding in harsh environments.

In a biparental system the cost of incubation is paid by the individual parent, but fitness benefits of more successful reproduction is shared (Lessells & McNamara 2012). Therefore, sexual conflict over effort may arise between the assumedly unrelated parents (Lessells & McNamara 2012; Trivers 1972). Such conflict does not only arise for the incubation period in general, but may vary with different costs of incubation and benefits of off-nest behaviour throughout the day (Bulla et al. 2015). Although biparental incubation by both parents is present in around half of avian families and the majority of non-passerine species, studies of how parents divide duties over time and variation between pairs are deficient (Bulla et al. 2014; Marasco & Spencer 2015).

The Black Skimmer (*Rynchops niger*) is a piscivorous bird species breeding on the American continent, and is one of the few species nesting on the river beaches in Amazonia (Gochfeld 1978). In the United States it has been shown that the species has biparental care and males and females both participate in incubation (Burger 1981a; Quinn 1990). Additionally, compared to other closely related species, sexual size dimorphism is particularly pronounced (Coulson 2001), and differentiating parental roles during breeding as consequences of the larger size of the male have been studied (Burger 1981a; Burger 1981b; Quinn 1990). Varying incubation proportions by males and females were found in these studies, with larger predation pressure suggested for causing higher male incubation rates at some sites (Burger 1981a; Quinn 1990). However, in these studies limited observations were made at night, and therefore variation across the diel period is not taken into consideration.

Habitat selection studies of the species have been carried out in two sites in the Amazon, the Manu National Park in Peru (1987 to 1988; Groom 1992; 2013), and Anavilhanas Archipelago in Brazil (2008 to 2009; Zarza et al. 2013). Black Skimmers were found on only some of the beaches surveyed, suggested to indicate active selection choices between beaches with different biotic and abiotic factors

(Zarza et al. 2013). Black Skimmers are often colonial species, with colony sizes reported from the Amazon varying, but single nesting pairs on beaches have also been observed (Groom 2013; Krannitz 1989; Raeder & Bernhard 2003; Zarza et al. 2013). However, to the best of my knowledge, habitat, nest site selection and nesting success, are the only aspects of nesting behaviour studied for the species in the Amazon. Therefore, studying the Black Skimmer incubation behaviour on the open beaches in the Amazon, allows for gathering of further knowledge on how a species with biparental care is adapted to a hot, tropical environment. Apart from presumably having to cope with a heat stress, predation pressure has been shown to be high (Groom 1992; Groom 2013), possibly affecting gender roles during incubation.

This study was carried out in the Manu National Park. This might be an ideal site for nesting behaviour studies of Black Skimmers due relatively little human disturbance (Gentry & Terborgh 1990; Ohl-Schacherer et al. 2007), which has been suggested to affect distributions of these birds elsewhere in the Amazon (Raeder 2003, Zarza et al. 2013). Furthermore, the lack of long-term research of vertebrates in the western Amazon results in population trends largely going unnoticed (Pitman et al. 2011). Although the species is listed as ‘Least Concern’, there are indications of decline (del Hoyo et al. 2014; IUCN 2016), including in parts of the Amazon (Caputo et al. 2005). The Black Skimmer has been suggested as a suitable indicator species of changes to their riverine habitat (Pitman et al. 2011) and transfer of findings from the Manu can be applied to conservation of the species at rivers lacking research.

The study had multiple aims. Firstly, it was aimed to build on current knowledge of habitat selection for nesting by Black Skimmers in Manu National Park, specifically what abiotic and biotic factors might determine habitat and nest site selection. Secondly, to determine whether there is evidence for high temperatures affecting incubation by comparisons of beach surface and nest temperatures, as well as observations of incubating adults. I hypothesized that nest temperatures are kept constant irrespective of temperature fluctuations on the beach surface, at the expense of thermal stress in incubating adults. Thirdly, to test for incubation behaviour patterns with temperature, time of day and incubation progress, as well as more specifically patterns in male and female share. Here I hypothesized that male Black Skimmers incubate a larger proportion of time than females and that incubation is shared most equally in any diel periods that might be thermally stressful.

2. Methodology

2.1 Site description

2.1.1 The Manu River

Research was carried out along the Manu River, located in the southeastern Peruvian Amazon. The entire watershed is protected within the Manu National Park (Gentry & Terborgh 1990; Figure 1). The park's remoteness and very low human population, as well as strict regulations against commercial activity, have ensured considerably less disturbed biological communities than other parts of the Amazon (Gentry & Terborgh 1990; Ohl-Schacherer et al. 2007; Shepard Jr et al. 2010).

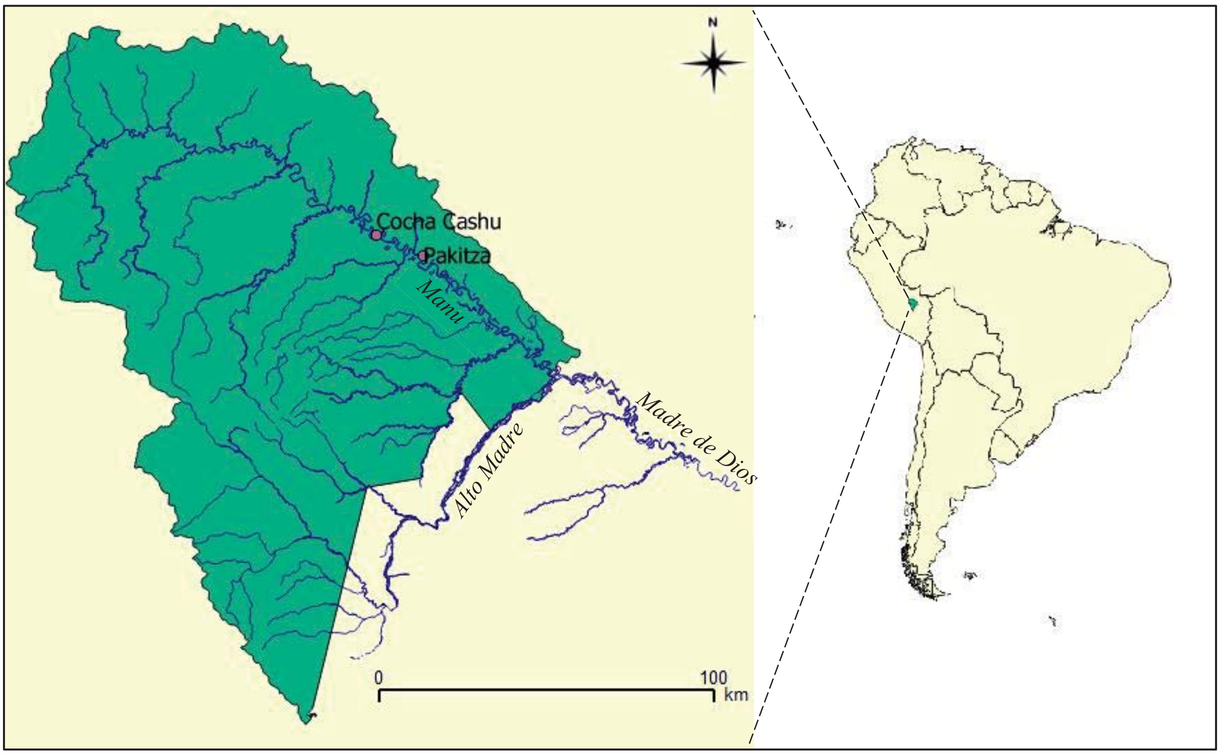

Figure 1: The Manu National Park in southeastern Peru, protecting the whole wathershed of the Manu River (Adapted from shapefiles sourced from the 'Servicio Nacional de Áreas Naturales Protegidas por el Estado')

The headwaters of the Manu River originate in the Andes in the west and lowland forest in the east (Osorio et al. 2011). It is a white-water river as a consequence of a high sediment load from the Andes, and therefore sustains high aquatic productivity (Fittkau et al. 1975; Osorio et al. 2011). The 100-200m wide Manu River joins the larger Alto Madre de Dios River after meandering across the Manu lowland floodplain (Groenendijk et al. 2014; Figure 1). Annual rainfall is approximately 2000mm, but only around 5 % of rain fall between June and October (Terborgh 1990; Figure 1). Thus, the river water level drops considerably in the dry season between May and October, exposing several sandy beaches along the river banks on the inside of meander loops (Groom 1992; Robinson & Terborgh 1997). They are up to two km in length (Davenport et al. 2016), but size and distance between beaches varies (Groom 1992). Nevertheless, the proximity to the Andes causes a less predictable flooding regime than in the central

Amazon (Robinson & Terborgh 1997), with frequent rapid flood pulses even during the dry season (Davenport et al. 2016; Osorio et al. 2011).

2.1.2 Fieldwork Setting

The study took place from 4th June to 30th September 2015, coinciding with the dry season and the breeding of Black Skimmers along the Manu River (Groom 1992). I was based at Cocha Cashu Biological Station (11°53'17.38"S 71°24'27.02"W, 350m masl), and all beaches with nesting birds were reached by boat. The core study area, where incubation behaviour observations were made, covered approximately 38km of the Manu River and entirely within the biological station's research zone (Figure 2). The research zone is bordered at one end by a "Special Use Zone" where subsistence hunting and harvesting by indigenous people are permitted, and at the other end by a "Tourist and Recreation Zone" allowing for ecotourism activities (Shepard Jr et al. 2010). No such activities are allowed in the Cocha Cashu research zone. Thus, the only source of anthropogenic disturbance to birds breeding on the beaches is the occasional passing of boats to and from Cocha Cashu and to the indigenous communities found upriver. In addition to the 38km core study area, another 16km downriver were surveyed less regularly, 10km of which extended past the Pakitza guard post and into the zone allowing tourist access (Figure 2). However the majority of tourists do not travel this far upriver and even here disturbance levels are low (Shepard Jr et al. 2010).

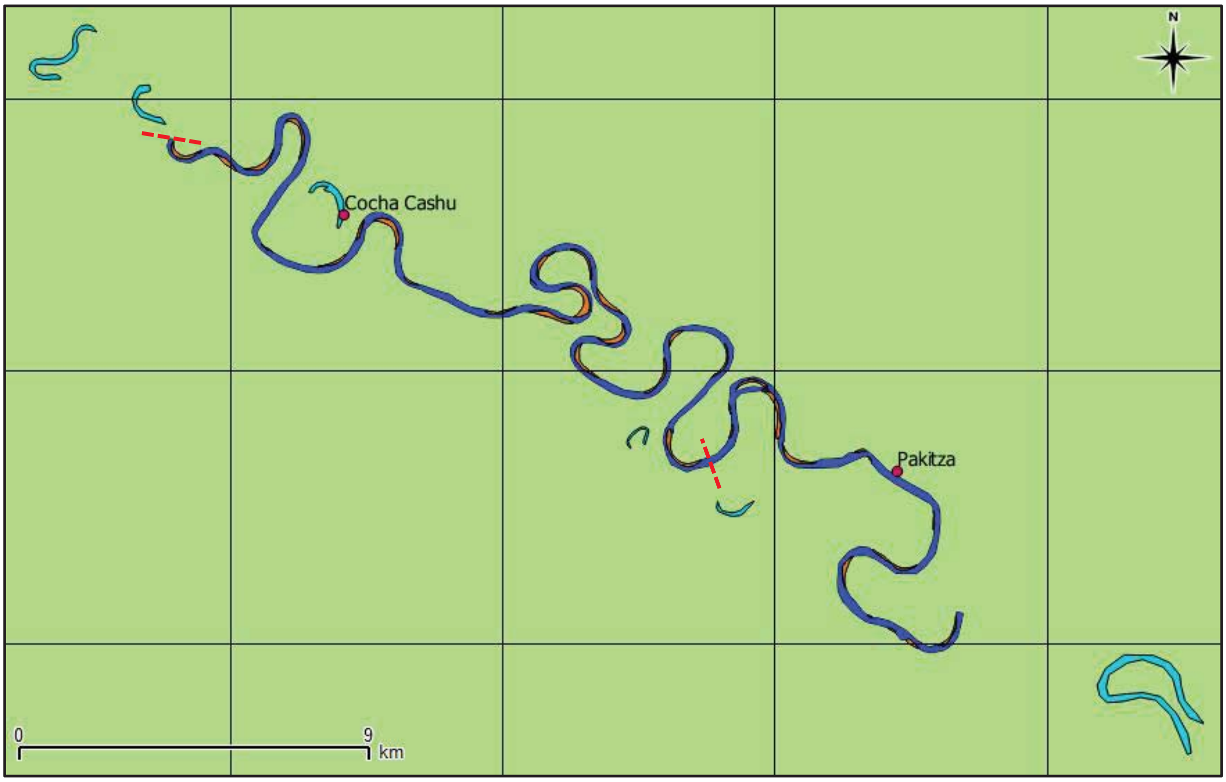

Figure 2: Map of the field study area, only showing the part of the Manu River surveyed. The 38km long core study area where behaviour of incubation birds was studied is the section delineated with dashed red lines. Pakitza guard post is shown, below which the "Tourist and Recreation Zone" started. All the beaches present in the fieldwork period are shown in orange as traced by GPS in the field. Oxbow lakes with open water are shown in light blue, while side rivers to the main channel are not shown.

2.2 Beach and Nest visits

2.2.1 Visits to the core study area

The average visit frequency to beaches in the core study area was 2.5 day (±0.9 Standard Deviation; SD). Daily visits were made to some beaches during short periods, while other beaches more than 12km from Cocha Cashu were visited every 3-5 days due to fuel constraints.

Nests were located by passing beaches slowly by boat and searching the part of the beach where birds were observed. Eggs were laid directly onto the sand in shallow depressions (Figure 3). Black Skimmers are known to make several depressions as part of courtship behaviour (Gochfeld 1978; Grant & Hogg 1976), but beaches were searched well to make sure no active nests were present. GPS nest positions were taken with a handheld 'Garmin etrex vista HCx' with an accuracy of ± 3 metres.

Figure 3: Black Skimmer nest with three eggs. Eggs are laid directly on the sand in a shallow depression.

Mean beach/nest visit time was 22min, with maximum of 1h, and an attempt was made to visit nests as early in the morning as possible. Nevertheless, due to travel time between beaches, the last ones were often visited around midday. On cloudless days, visits after 10:00am were kept short to reduce heat stress to nests.

2.2.2 Beach choice

To examine whether Black Skimmers exhibited beach selection, the entire study area was surveyed (Figure 2). Nesting on the beaches beyond the core study area was determined by searching beaches for active nests on four trips, distributed across the study period. The searches were conducted during periods of breeding activity observed on beaches that were more regularly visited.

Two separate presence/absence categories were created for nesting attempts on each beach. One determined whether at least one nesting attempt took place. The other determined whether nesting occurred at least twice at different times throughout the season (non-simultaneous attempts). Presence/absence notation makes sense in colonial species, for which only the first pair to colonize a site seem to make habitat choice decisions and therefore the number of pairs might be irrelevant (Heinanen et al. 2008). However, the number of active nests per beach visit was also recorded.

Five measurements characterizing beach size were taken: shore length, beach area, area of non-vegetated beach surface, beach width and beach height. Complete perimeters of all beaches in the entire study area were traced using a handheld GPS, between the 23rd and 26th August. River level variation was minimal during this period. The beach shore, defined as the edge of the beach with the river, was traced separately from the beach rear. The latter was defined as the transition between beach sand to vegetated mud bank. QGIS Desktop 2.14.1 (QGIS Development Team 2016) was used to find the shore length and beach area. In addition to vegetation on mud banks, where beaches end, vegetation grew on the sand of some beaches. Vegetated parts of the sandy beaches were also traced, to then calculate area of non-vegetated beach. Furthermore, the beach width, (defined as perpendicular distance between shore and rear), was measured manually in QGIS at the widest point of the beach.

Beach height was only measured for the beaches in the core study area. This measurement was conducted using two vertical wooden stakes of equal length inserted into the sand up to a pre-marked notch, onto which a horizontal strip of wood 2m in length was placed. The angle of the horizontal strip was measured with a digital clinometer to the nearest 0.1^0. The setup was moved from the river edge to create a continuous profile across the beach, angles being converted to height in metres through trigonometry. High banks on the far back of beaches were not included in height measurements as these were small and not representative of the beach. River level was corrected for in beach height. River level was measured to the nearest 0.1cm as the vertical distance between the river to a string tied to a fixed mark on the bank. The string was kept parallel to the river using a spirit level. The difference between river level on the day beach height was measured and the day with lowest river level was added to beach height to standardize measurements.

Additionally, distances between beaches and distances from beaches to oxbow lakes was measured. The distance matrix tool was used to find the mean direct airline distance to the two closest beaches from each beach. To account for the possibility of social attraction in beach selection, the distance to the closest beach supporting nesting Black Skimmers at least once in the season was calculated. Google Earth imagery was used in locating oxbow lakes and determining the ones that had open water surfaces adequate for Black Skimmer foraging (Willard 1985). Six oxbow lakes were included (Figure 2). The NNJoin QGIS plugin was used to calculate the airline distance from beaches to the nearest oxbow lake.

2.2.3 Nest site Selection

Nest site selection measurements relate to where on beaches Black Skimmers chose to nest. Distance to the river edge from nests was measured with a measuring tape during the egg-laying period. Height above the river level of 12 nests, active in the end of August and in September, was measured as described in section 2.2.2 and again corrected to the lowest river level. Additionally for ten of these nests, found during egg-laying, height was also corrected to the respective egg-laying dates.

Shortest distance from nests to the beach rear was found through the NNJoin tool in QGIS. This method was assumed more accurate than using a measuring tape, due to the larger distances involved. Additionally, distance from a nest to its nearest neighbouring nest found on the same beach, was measured with a 50m measuring tape for nests <50m apart or using the NNjoin tool in QGIS.

2.3 Temperature data

2.3.1 Nest Temperature

I used DS1921G Thermochron *i*Buttons® to measure temperature inside nests at an interval of every 20 min. *i*Buttons® are very small devices containing both a temperature logger and power source in the same casing. The *i*Buttons® used, record temperature at an accuracy of $\pm 1^{0}$C and resolution of 0.5^{0}C (Maxim Integrated Products 2015). *i*Buttons® were placed in the bottom of the nest under the eggs, covered slightly by sand in order to avoid detection by incubating adults. The loggers were placed in small zip-lock bags to prevent water and humidity damage, since they are only water resistant (Maxim Integrated Products 2015). Moreover, the *i*Buttons® and bags were covered in a thin polyester mosquito netting to reduce visible shininess of the steel casing, an additional measure to avoid detection by adults. As in other studies the loggers were secured on long nails driven into the sand substrate, with the *i*Buttons® at the top closest to the nest. This facilitates retrieval and reduces movement in the nest (Cervencl 2011; Schneider & McWilliams 2007; Hartman & Oring 2006).

For comparison, other *i*Buttons® were placed outside nests on the beach surface, just covered by a thin layer of sand in the same netting and zip lock bag covering, for comparison with nest temperature (Cervencl 2011; Schneider & McWilliams 2007). Comparisons were only made between nest and beach surface *i*Buttons® placed on the same beach. Additionally comparison was made between two inactive (abandoned) nests and two active nests during the same specific dates. The number of eggs in the nests was also the same. This comparison allowed for testing whether differences in temperature was due to the position of *i*Buttons® at the bottom of the nest or due to incubation.

2.3.2 Temperature gradient across beaches

Transects across beaches were created to test the hypothesis that the river has a thermal regulation effect on nests placed close to the river edge (Davenport et al. 2016; Groom 2013). Twenty-eight *i*Buttons® were placed in three transects on separate beaches, starting from two to four metres from the shore edge and continuing, perpendicular to the river, at an interval of ten metres across the beach. They recorded surface temperature of the beach at five-minute intervals between 3rd September 12:00 and 9th September 08:00. Height of the beach was measured at every *i*Buttons® placement as described in 2.2.2.

2.4 Incubation behaviour: Camera trapping

Bushnell Trophy Cam HD (Bushnell Corporation, Overland Park, KS, USA) and Reconyx HC500 Hyperfire (Reconyx Inc., WI, USA) camera traps were deployed in a rotation system to record behaviour at nests. Infrared LED flash on the cameras allowed for night time recording, an improvement to other behaviour studies of Black Skimmers (Burger 1981b; Quinn 1990). The Bushnell cameras had no-glow flash, and the Reconyx a low-glow flash, which substantially reduce visible red light and therefore detection by both nesting birds and potential predators (Rovero et al. 2013). Moreover, camera traps were equipped with built-in passive infrared receivers that trigger the camera when changes in radiant infrared is detected (Cox et al. 2012). However, motion detection can be random, trigger rate varying with surface temperature of surroundings (Cox et al. 2012; Rovero et al. 2013; Welbourne et al. 2016). To ensure continuous recording, cameras were also set on timelapse mode and images taken every minute. This is the most frequent rate allowed by the cameras.

Cameras were placed at a distance of five metres from nests, tied to a small stake and elevated slightly on a mound of sand (Figure 4). Black Skimmers have been shown to react aggressively to objects placed within one metre of the nest (Grant & Hogg 1976). Five metres was therefore chosen to obtain sufficiently good images while attempting to cause the least disturbance to incubating birds. While two out of 35 nests were abandoned after camera trap placement and another two pairs were captured in images attacking cameras physically, all pairs included in analysis continued to incubate and did not attack cameras.

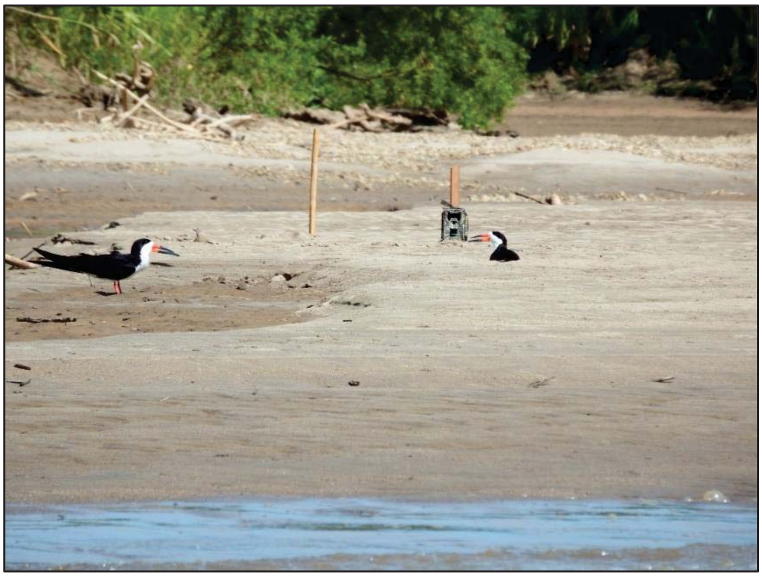

Figure 4: Black Skimmer pair at nest. The bird on the right is incubating and the camera trap is deployed at a distance of five metres from the nest facing the river.

2.4.1 Days until hatching

On each nest visit, the number of eggs was counted, which allowed me to determine the approximate date when egg-laying was complete (Dinsmore 2008). The number of nestlings were also counted when hatching started. It was assumed that order of hatching followed order of laying, since asynchronous hatching is displayed in Black Skimmer nests (Grant & Hogg 1976). Following this assumption, the median number of days for an egg to hatch was calculated for 19 eggs from nine nests (mean visit frequency between 1.8 and 2.7 per nest). This median number was then used to approximate days until hatching for nests that did not reach hatching due to flooding but for which I had egg-laying dates.

For the three nests with the lowest visitation frequency and unrecorded hatching dates, an egg flotation model was used to predict days until hatching. Egg flotation was carried out in line with the method described by Liebezeit et al. (2007) and Mabee et al. (2006). Eggs were placed in a clear container with river water, recording the angle between the bottom of a container and the egg axis, as well as the height in mm above the water surface. The measurements used to create the model were acquired from 11 nests with observed hatching dates (mean visit frequency between 1.8 and 3.3 per nest). Flotation was carried out throughout the incubation period, except for a few days before expected hatching. Some eggs were floated on more than one visit as suggested by Liebezeit et al. (2007) to increase model accuracy. Flotation angle and height were then entered as explanatory variables into a linear regression model (Table 1).

Table 1: Parameter estimates of egg flotation model used for prediction of days until hatching. The model is based on 11 nests with known hatching dates. Measured angle and height above surface of eggs are explanatory variables of days until hatching.

Variable	**Estimate**	***SE***	***DF***	***P***
(Intercept)	25.369	1.271	10	< 0.001
Angle	-0.175	0.021	4	0.001
Height above surface	-1.221	0.392	4	0.036

In summary, the variable days until hatching is an approximate for each nest based on either direct observations, the estimate for incubation period or the flotation model, as perceived most accurate with the data available for each nest.

2.4.2 Image Analysis

Image data from camera traps were divided into three parts. Firstly, the egg-laying period during which Black Skimmers incubate (Dinsmore 2008). Secondly, the incubation period, defined here as being between the date when the largest clutch was recorded and the first egg hatched and finally, the hatching and nestling period. Since most data were gathered for the incubation period, the analyses herein are limited to this part. Black Skimmer nestlings tend to move out of the nest just a few days after hatching (Quinn 1990; Safina & Burger 1983), so obtaining data for the brooding period with camera traps is difficult.

Moreover, data were divided into three separate nesting attempts (A1, A2, A3), as a consequence of two major flash floods (9th July and 10th August) that destroyed all nests being studied at the time. Image data obtained for A1 (29th June – 08th July) only covered the egg-laying period and was therefore not included in the analysis. In A2 (13th July to 9th August), nests were at the end of the incubation period or in the hatching period when flooded. Therefore, A2 and A3 (19th August to end of fieldwork period 30th September) were analysed, although each nesting attempt was analysed separately to avoid pseudoreplication. It is likely that at least some of the birds were the same from one nesting attempt to another, since Black Skimmers tend to re-nest after nest failure (Gochfeld 1978; Groom 2013).

Due to unequal coverage across the day of motion triggered images, only timelapse images, taken each minute, were included in the analysis. A nest was included in analysis only if a minimum of a 24 hour period of images was obtained. Up to 96 hours was analysed per nest. For some nests even more data were obtained, but not analysed due to viewing time constraints. In such cases 24-hour periods of images were selected prior to viewing, distributed evenly over the entire range of days with data. This resulted in 44395 images for A2 covering nine nests on eight beaches (Table 2), and 37331 images for A3, for eight nests on five beaches (Table 3).

Table 2: Number of images for the nine nests of the second attempt (A2), found on eight beaches.

A2

Beach ID	**B820**	**B810**	**B800**	**B780**		**B770**	**B750**	**B720**	**B680**
Nest ID	N3 B820	N1 B810	N2 B800	N2 B780	N3 B780	N1 B770	N1 B750	N2 B720	N1 B680
Images	5539	5702	5826	4285	5720	1451	5859	4553	5460

Table 3: Number of images per the eight nests of the third attempt (A3), found on five beaches.

A3

Beach ID	**B830**	**B780**		**B760**	**B720**	**B680**		
Nest ID	N1 B830	N4 B780	N5 B780	N5 B760	N3 B720	N4 B670	N3 B680	N6 B680
Images	5802	5713	4321	5778	5620	2883	4321	2893

XnView 2.34 was used to view images. This program has the advantage of being able to display several image panes next to each other, allowing for better determination of bird gender. Male and female Black Skimmers can be distinguished in the field based on features such as size as well as length and depth of beak (Burger 1981b; Quinn 1990). Gender was determined in 96.14 % of images with incubating birds. Thus, for each image the following was recorded: the presence/absence of an incubating bird (Figure 5),

the gender when possible, whether the incubating bird extended its neck and head upward (Figure 5a & b) and whether the incubating bird turned its head and kept the beak between the scapular feathers in a sleeping posture (Figure 5c). The extended neck behaviour can be an indication of heat stress and alertness in birds (Amlaner & Ball 1983; Bartholomew & Dawson 1979). Time was timestamped on each image and extracted from the image metadata using RStudio (© 2009-2015 RStudio, Inc.) linking to ExifTool-10.07 (Harvey 2016).

Incubation bout length was also calculated, albeit with a one minute error due to use of timelapse images taken at one minute frequencies (Smith et al. 2015). An incubation bout is defined here as consecutive images with the same bird incubating, and calculated by subtracting the time of the first image in a bout from the last one. Single images with an incubating bird, were given a bout length of one minute. It is assumed that incubation bouts shorter than one minute were unlikely. Bouts disrupted by nest visits and passing boats documented in images were eliminated. Bouts with uncertain length due to periods where the gender of the incubating bird was unidentified, were also removed before analysis. This resulted in 1705 and 1807 incubation bouts in A2 and A3, respectively.

Figure 5: Camera trap images from the same nest. In a) the female is incubating, with visibly shorter and thinner beak as well as smaller size than the male in b). Both birds in a) and b) are in the position recorded as extended neck. The bird in c) is the male in a sleeping posture with beak lying between the scapular feathers.

2.5 Statistical Analysis

RStudio 0.99.491 (©2009-2015 RStudio, Inc.) run with R version 3.2.2 and 3.2.4 Revised (R Development Core Team 2011-2016) was used for statistical analysis and graphical representations if not otherwise stated.

2.5.1 Beach choice

Generalized Linear Models (GLMs) were used to test which habitat factors may influence nesting beach choice. The presence/absence of whether Black Skimmers nested at least once on a beach was the response of one set of models. Whether more than one non-simultaneous nesting attempt occurred was the response variable in a second set of models. A binomial distribution was used in the GLMs due to the binary nature of the responses. The explanatory variables 'beach area', 'area of non-vegetated beach', 'beach width' and 'shore length', all being positively correlated (>0.7), were not entered into the same models. Instead they were run in separate models, each with the additional non-correlated variables 'distance to closest beach used by nesting Black Skimmers', 'mean distance to the two closest beaches' and the 'distance to the closest oxbow lake'. Beach height was not measured for all beaches and therefore not run in GLMs.

The 'dredge' function in the 'MuMIn-package' was used to select the best model(s) from combinations deriving from each of the global models. The dredge function incorporates 'Second-order Akaike Information Criterion' (AIC_c) for model selection (Bartoń 2016), which is a modified version of the Akaike Information Criterion (AIC), suggested for small sample sizes (Burnham & Anderson 2004; Burnham et al. 2011). The dredge function presents the model with lowest AIC_c value. However, models with less predictor variables and $\leq \Delta 2.0$ AIC_c of the model with lowest AIC_c, were also included in a final ranking of models (Arnold 2010; Burham & Anderson 2004; Burnham et al. 2011). The final AIC_c ranking of the resulting models was carried out using the 'AICcmodavg-package' (Mazerolle 2016). This is possible because models do not need to be nested when using an information criterion method (Bolker 2008). The 'predict' command was used to obtain the probabilities of beach choice as modelled by the GLMs (Zuur et al. 2009).

2.5.2 Temperature gradient across beaches

Temperature data were used to test for a trend of temperature range with height and distance from river edge. Data were divided into two periods reflecting approximately day and night, from 07:00 to 17:59 and from 18:00 to 06:59, respectively. Statistical analysis was limited to the day period, when the highest temperatures occur. Standard deviation of temperature readings for each *i*Button® was calculated and entered as response in two separate simple linear regression models because the two explanatory variables distance and height were correlated. Distance and height were natural log transformed to improve model fit. In the models, a single data point showed up as having high influence in diagnostic plots. Thus models were repeated without this data point, as suggested by Crawley (2013).

2.5.3 Nest Temperature

Whether any temperature differences between nests and beach surface were simply due to the nest logger being covered by eggs and positioned at the bottom of a nest was tested. Comparison was made between two inactive nests and two active nests. The two abandoned nests used in this comparison contained two and three eggs respectively, as did the active nests. A non-parametric Mann-Whitney U-test for paired data was used. Since the data was from the exact same time period, the test was run for paired data.

2.5.4 Incubation behaviour

In order to determine whether incubation behaviour varies with progression of the incubation period and through a 24-hour diel cycle, statistical models were applied to the different behaviour categories observed in camera trap images. To account for the non-independence of images from the same nest, a random effect should be used (Crawley 2013). Moreover, the responses to be tested were non-normal. Therefore, generalized linear-mixed models (GLMMs) were applied, permitting inclusion of random effects (Bolker et al. 2009). The 'lme4-package' was used (Bates et al. 2016). For A3, because two beaches had two and three of the nests respectively (Table 3), 'Nest ID' was entered as a nested random effect of 'Beach ID' (Bolker et al. 2009). For A2 a single 'Nest ID' random effect was sufficient.

Response variables

Four sets of GLMM models were run with different response variables. The first response was the presence/absence (1/0) of an incubating bird in each image. For the second and third responses the dataset was restricted to images with incubating birds only. The second response was the presence/absence (1/0) of the sleeping posture in incubating birds. The proportion of male incubation per hour was the third response. In calculating proportions, images in which gender was not identified were removed. GLMMs for these three responses, were run with a binomial family distribution (Bolker et al. 2009). The fourth response was incubation bout length. Due to a strong left skew, negative binomial GLMMs were used, improving on a Poisson family distribution (O'Hara & Kotze 2010).

Explanatory variables

The effects of time of day, ambient temperature, days until hatching and progression through the season on the abovementioned responses were tested for. To test for any patterns across time of day, decimal hours were entered into sine and cosine equations, known as cosinor functions (Pita et al. 2011). Three different sets of functions, each with added cosinor components to the previous one were used. This multiple component approach made it possible to test for different levels of sinusoidality, because the day is also divided into shorter periods rather than just modelling a full 24 hour wave (Cornelissen 2014; Fernandez et al. 2009; Pita et al. 2011). The cosinor components used were as follows, each numbered set of functions being entered separately into models:

i) I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24))

ii) I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24))+I(cos(2*2*pi*Hour/24))+
I(sin(2*2*pi*Hour/24))

iii) I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24))+I(cos(2*2*pi*Hour/24))+
I(sin(2*2*pi*Hour/24))+ I(cos(3*2*pi*Hour/24))+I(sin(3*2*pi*Hour/24)).

Ambient temperature recordings, taken every five minutes were obtained from the Pakitza weather station (11°56'45.83"S 71°16'47.71"W), managed by the 'Tropical Ecology, Assessment and Monitoring (TEAM) Network'. Days until hatching is explained in 2.4.1. Yet another explanatory variable, 'Days after Julian Day', indicated season progression and is defined as the number of days after the 1.06.2015. The latter was not entered in A3 models because of higher nesting synchrony of the eight nests analysed for the attempt. This meant that there was strong correlation (-0.73) with days until hatching. On the other hand, correlation between the two variables was -0.34 in A2. Nevertheless even for A2 models, the two variables were not entered into the same models. Other than this exception, all combinations of the mentioned explanatory variables were entered in each set of GLMMs with incubation, sleeping posture and proportion of male incubation as response variables respectively. For the models with incubation bout length as response, effect of days until hatching and days after Julian day was not tested for. However, whether the bout was carried out by a male or female was included as an explanatory variable, while ambient temperature was log transformed. Finally, for all response variables, null models with only random effects were included.

All models were fitted using the default Laplace Approximation which finds parameter maximum likelihood estimates, attempting to give values that describe the highest probability that the observed data occurred (Bates et al. 2016; Bolker 2008; Bolker et al. 2009). When models failed to converge the 'bobyqa' optimizer from the 'minqa-package' (Bates et al. 2015), was added to increase maximum number of evaluations possible (Bates et al. 2016).

Model Ranking and Prediction

The 'AICcmodavg-package' (Mazerolle 2016) was used to rank models. The most parsimonious model $\leq \Delta 2.0$ AIC_c of the model with lowest AIC_c was chosen for prediction (Arnold 2010; Burham & Anderson 2004). Through prediction carried out on the range of values present in the dataset, model outputs could be viewed visually. The 'predict' method in the lme4-package was used (Bates et al. 2016). In addition to prediction values, 95% confidence intervals (CI) were calculated. Both predicted values and their CI are at the entire sample level because random effects are not considered with this method (Bates et al. 2016; Bolker 2015). Additionally model overdispersion was tested for, using the ratio of Pearson residuals to residual degrees of freedom. For models with slight overdispersion, predictions and intervals were plotted against the actual data to access model fit visually (Zuur et al. 2009).

Predictions were often calculated for models with several explanatory variables. In these cases, predictions and CIs were produced on all combinations of explanatory variable values. However in producing graphs, the mean prediction and CI values were calculated per unit value of the explanatory variable to be presented. Thus, although only one explanatory variable is presented in each graph, the other explanatory variables in the model are still accounted for. Moreover, in some cases predictions and CIs were calculated for only one value of an explanatory variable, for example predicting diel pattern for a maximum temperature value.

Finally, the ‘midline estimated statistic of rhythm’ (MESOR), which indicates mean level of activity across the entire diel period, was predicted using the null models (Pita et al. 2011). Increased or decreased activity predicted by cosinor functions, can be identified as significant in parts of the diel period where 95 % CI do not overlap MESOR (Refinetti et al. 2007).

3. Results

3.1 Beach Choice

In total, 35 beaches were present in the dry season along the surveyed stretch of the Manu River. Considerable variation in their features were evident (Table 4), especially in the measurements relating to beach size. Height of beaches above the lowest river level also varied between the measured beaches, ranging from 0.86m to 4.35m, with a mean of 2.16m (±1.06 SD).

Table 4: Descriptive summary of seven beach variables measured for all 35 beaches along the survey stretch of the River Manu, Peru.

Beach Variable	Min	Max	Mean	SD
Total Beach Area (km^2)	0.003	0.133	0.044	0.032
Area of non-vegetated beach (km^2)	0.003	0.099	0.042	0.029
Width (m)	28.93	195.32	85.60	39.58
Length (m)	188.0	1843.0	1001.71	450.94
Distance to closest beach used by nesting Black Skimmers (km)	0.344	3.640	1.483	0.768
Mean distance to two closest beaches (km)	0.634	1.863	1.159	0.320
Distance to closest oxbow lake (km)	0.855	4.949	2.718	1.837

Black Skimmers did not nest on all beaches available, exhibiting preference to some beaches. Sixteen beaches (46 %) were used for nesting at least once throughout the season. Beach width seems to be the most important variable of the correlated beach size variables in determining selection by Black Skimmers (Table 5). Wider beaches had a significantly higher probability for selection (Table 7; Figure 6). The probability of selection is also slightly higher if a beach is further away from a beach used by nesting Black Skimmers, albeit the effect was not significant (Table 7; Figure 6).

Moreover, ten beaches (29 %) were used in more than one non-simultaneous attempt. Three of the four beach size variables seem to affect the probability of beach re-use, being within Δ3 AIC_c of the best ranking model (Table 6). However, beach width is again the most important explanatory variable and wider beaches have significantly higher probability of re-use (Table 7; Figure 7). Although, three out of the five colour-ringed birds present in the study area, nested on the same beach for two consecutive attempts, beach re-use was not necessarily always re-nesting by the same pair. This was shown by the other two colour-ringed birds, which moved to a beach one kilometre downstream after their first attempt was flooded.

Table 5: AIC_c ranking of resulting best GLM models from four global models for beach choice, with the response variable being whether Black Skimmers bred at least once on a beach throughout the season. Model number is assigned post-selection in order to separate models in further presentation.

Model	Predictor variables in GLM model	K	AIC_c	ΔAIC_c	AIC_c Weights
1	Width + Distance to closest beach used by nesting Black Skimmers	3	24.12	0.00	0.97
2	Total Area + Distance to closest beach used by nesting Black Skimmers	3	32.55	8.43	0.01
3	Area of non-vegetated beach + Distance to closest beach used by nesting Black Skimmers	3	32.68	8.56	0.01
4	Shore Length + Distance to closest beach used by nesting Black Skimmers	3	44.11	19.99	0.01

Table 6: AIC_c ranking of resulting best GLM models from four global models for beach choice, with the response variable being whether Black Skimmers bred more than once on a beach in non-simultaneous attempts. Model number is assigned post-selection in order to separate models in further presentation.

Model	Predictor variables in GLM model	K	AIC_c	ΔAIC_c	AIC_c Weights
1	Width + Distance to closest beach used by nesting Black Skimmers	3	27.08	0.00	0.46
2	Width	2	27.81	0.72	0.32
3	Total Area	2	29.96	2.88	0.11
4	Area of non-vegetated beach	2	30.05	2.96	0.10
5	Shore Length	2	34.57	7.48	0.01

Table 7: Parameter estimates of the GLM models for different responses reflecting beach choice by nesting Black skimmers in Manu National Park. Models presented are those with lowest AIC_c values and with AIC_c within Δ2 of these models, as presented in Table 5 and Table 6

Model	Variable	Estimate	*SE*	*P*	AIC
Response: P/A per beach of at least one nesting in whole season					
1	(Intercept)	-14.937	6.246	0.017	23.346
	Distance to closest beach used by nesting Black Skimmers	3.8022	2.040	0.062	
	Width	0.106	0.040	0.008	
Response: P/A per beach for more than one non-simultaneous nesting attempt					
1	(Intercept)	-11.875	5.149	0.021	26.31
	Width	0.088	0.034	0.027	
	Distance to closest beach used by nesting Black Skimmers	1.333	0.861	0.122	
2	(Intercept)	-8.368	3.379	0.013	27.43
	Width	0.073	0.030	0.014	

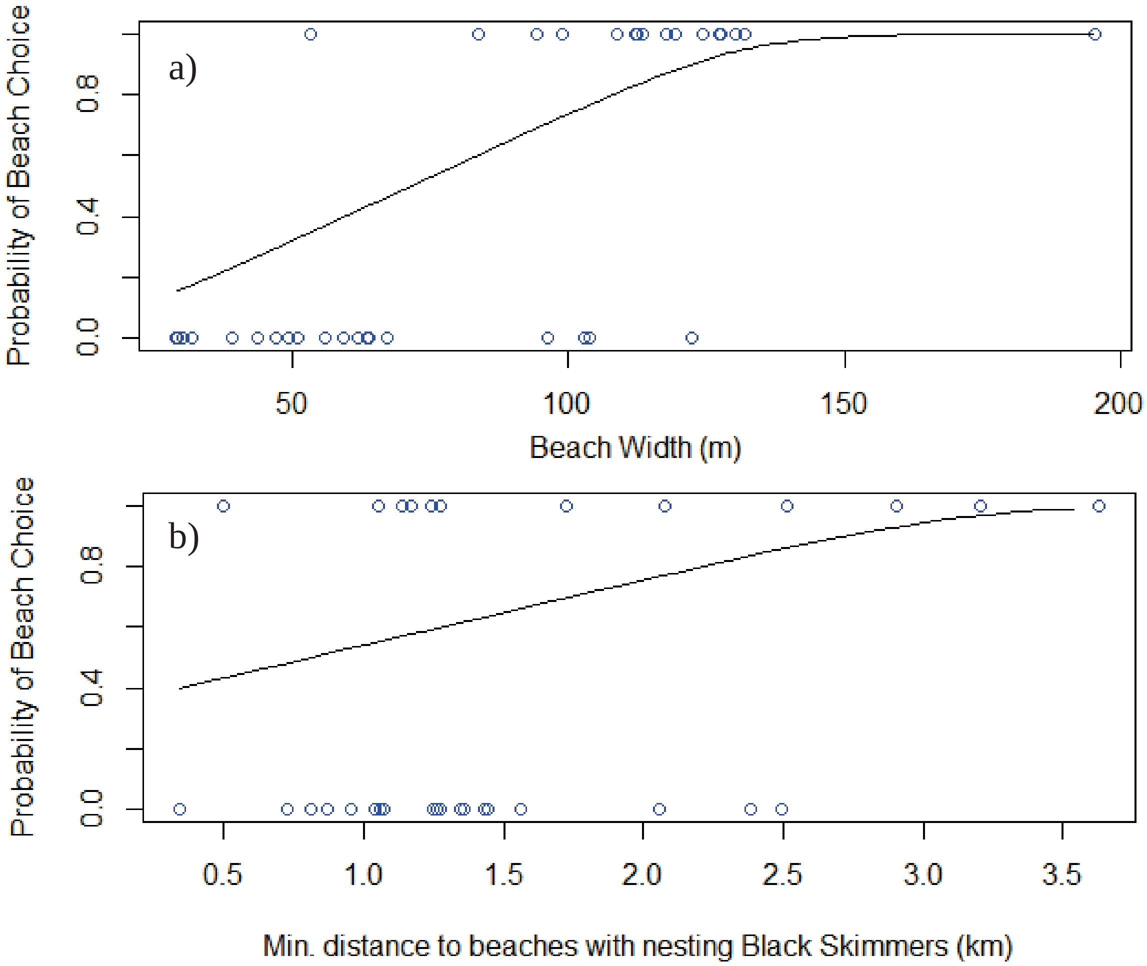

Figure 6: Predictions (solid line) from GLM model with the presence/absence response of whether Black Skimmers bred at least once on a beach throughout the season. Predictions are based on best ranking model in Table 5, parameter estimates presented in Table 7. Blue circles present the actual data on which model is based, points at y=0 are beaches where no nesting occurred, points at y=1 are beaches where nesting occurred. Probability of beach choice against width is given in a) and against minimum distance to closest beach with nesting Black Skimmers in b).

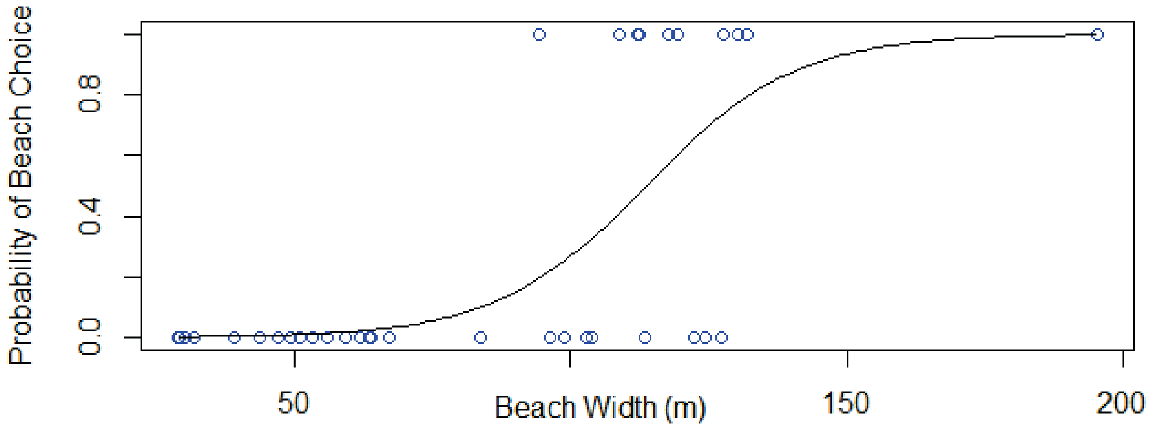

Figure 7: Prediction (solid line) from the GLM model with binomial response of whether Black Skimmers bred on a beach for more than one non-simultaneous attempt, and the explanatory variable beach width. Prediction is based on the most parsimonious model ≤ Δ2.0 AIC_c value of the model with lowest AIC_c. (Table 6). Parameter estimates for the model are given in Table 7. Blue circles present the actual data on which model is based, points at y=0 are beaches where nesting did not occur more than once, points at y=1 are beaches where nesting occurred for more than one non-simultaneous attempt.

3.2 Nest site Selection

Low nest densities were recorded per beach. Excluding beaches that were not used, the most common was one nest per beach, whereas the mean was two nests per beach (±1.46 SD). The highest number of active nests recorded on a beach was six. Furthermore distances between simultaneous nests (N=33) varied, with a mean distance of 120.4 m (±197.65 SD) between the two nearest neighbours on the same beach (median was 32.27m, minimum was 13.55m and maximum was 665.36m).

Nest site selection did not seem to be random in relation to habitat features. Black Skimmers nested at lower parts of beaches, and most pairs nested far away from the beach rear and vegetation on the beach itself (Table 8).

Table 8: Descriptive summary of nest sites selected by Black Skimmers along the Manu River in Peru. Distance to river edge was measured during the egg-laying period, and 'Height - egg-laying' was corrected to this period in respect to river level. 'Height – lowest level' is corrected to the lowest level of the river. The difference between the two 'distance to beach rear' measures is that for the second measure, distance to vegetation growing on the sand substrate where this was present, was measured instead. The number of nests on which the descriptive statistics are based is given for each measure.

	Min	Max	Mean	SD	Nests
Height – lowest level (m)	0.46	1.6	0.86	0.32	12
Height – egg laying (m)	0.26	1.42	0.61	0.33	10
Distance to beach rear (m)	27.48	159.25	78.59	25.07	53
Distance to beach rear or beach vegetation (m)	27.48	138.94	75.41	21.21	53
Distance to river edge (m)	5.00	43.60	19.29	9.67	29

3.3 Temperature gradient across beaches

Beach surface temperature ranges, as indicated by standard deviation of recorded temperature, increased with height and distance from the river edge (Table 9; Figure 8).

Table 9: Parameter estimates of linear models for standard deviation of beach surface temperature recorded by iButtons® during the time period 07:00 to 17:59 across six days in September 2015, run against height and distance from river edge. Reduced dataset models are the models run after the most influential data point (sourcing from an iButton® at height 0.13m height and distance 4m) was removed. .

	Variable	Estimate	Sdt. Error	Pr(>|t|)	Adjusted R^2
Temperature Standard deviation ~ log(Height)					
Complete dataset	(Intercept)	9.419	0.190	< 0.001	0.569
	log(height)	1.221	0.202	< 0.001	
Reduced dataset	(Intercept)	9.702	0.154	< 0.001	0.421
	log(height)	0.789	0.177	< 0.001	
Temperature Standard deviation ~ log(Distance)					
Complete dataset	(Intercept)	6.243	0.714	< 0.001	0.492
	log(distance)	1.011	0.194	< 0.001	
Reduced dataset	(Intercept)	7.605	0.537	< 0.001	0.444
	log(distance)	0.671	0.144	< 0.001	

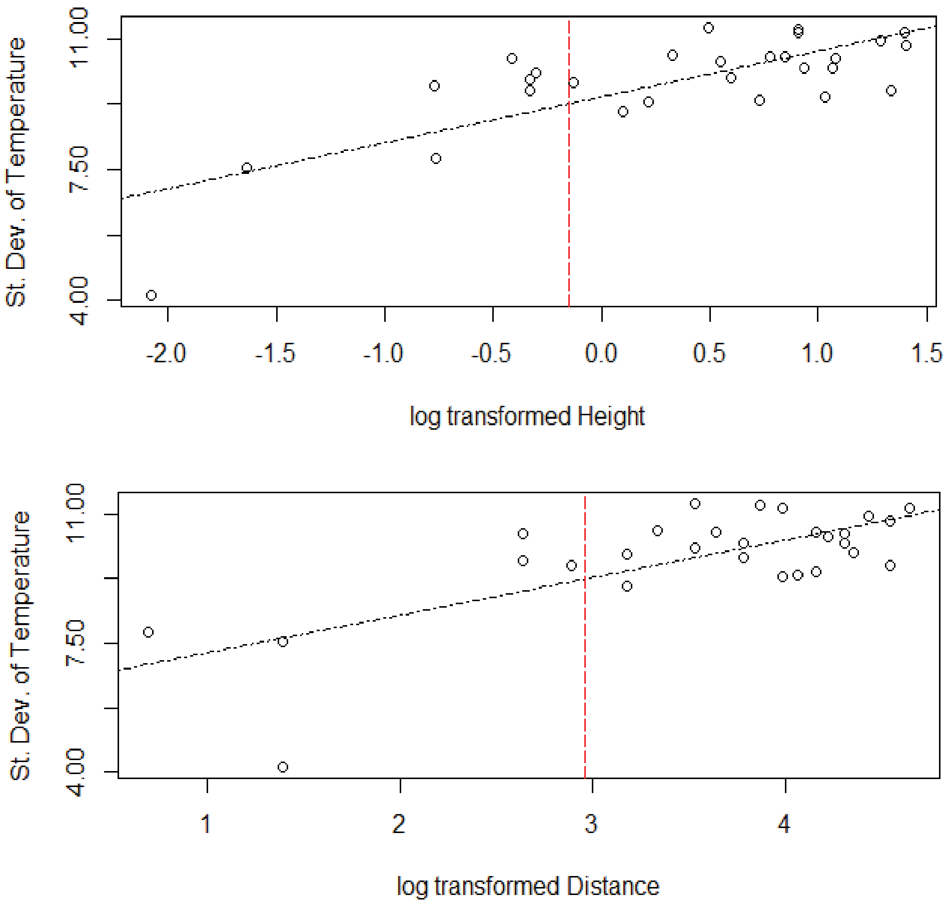

Figure 8: Linear regression lines (stippled black) for log transformed height and distance from river edge as explanatory variables of the standard deviation of temperature. Presented here are the models run on the full dataset. Parameter estimates are presented in Table 10. Actual data is shown in circles and the stippled red line represents the mean Black Skimmer nest site height and distance from the river.

3.4 Nest Temperature

Temperatures inside nests were more constant than temperatures recorded at the beach surface outside the nest (Figure 9). At night, nest temperatures were warmer than the beach surface, whereas the opposite was observed during the day. Overlap between nest and beach surface temperatures occurred on cloudy days when solar radiation was reduced, resulting in lower heating of the beach surface compared to sunny days. Overlap also occurred during the transition from night to day and day to night. In addition, temperature variability was significantly less in active nests than abandoned nests (Figure 10).

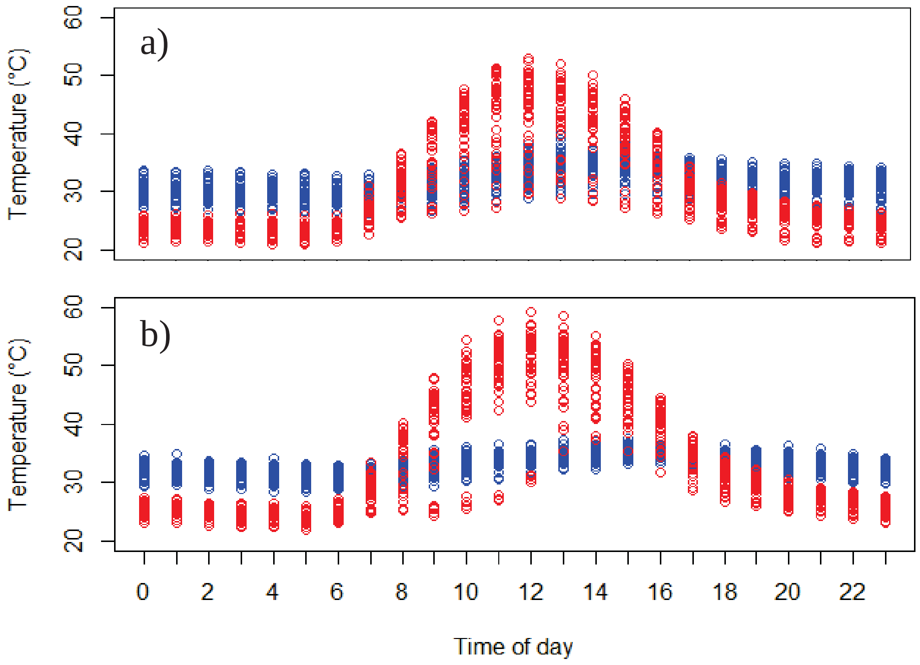

Figure 9: Average temperature per hour for inside nest temperature (blue) plotted against respective average per hour outside nest beach surface temperature (red). Temperatures from four nests in A2 are shown in a), and from six nests in A3 shown in b).

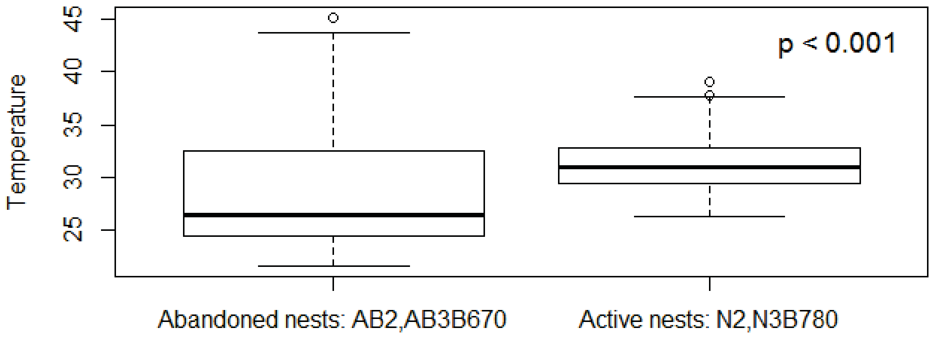

Figure 10: Comparison of *i*Button® recorded temperature inside two abandoned nests with temperature inside two active nests. The two abandoned nests contained two and three eggs, as did the active nests. The small *p*-value indicates a significant difference as produced by Mann-Whitney U-test for paired data, data being recorded during the same time period for all nests.

3.5 Incubation behaviour

Diel incubation patterns were very similar across the second and third attempts (A2 & A3; Figure 11), as predicted from the best ranked models selected using AIC_c (Table 10; Appendix 1). The Black Skimmers were found to incubate almost constantly, although at a lower probability around 17PM to 20PM. The highest incubation probability was around 22PM to 2AM. Moreover, incubation probability increased slightly as the incubation period progresses (days until hatching decrease), for both attempts (Table 10). Probability of incubation decreased with increasing ambient temperature in A3 (Table 10), although the difference does not cause significant changes to the diel pattern (Figure 12). Incubation models were slightly overdispersed (with maximum ratio of 1.07), probably due to the much larger amount of images with incubating birds than those without, but comparisons between prediction and actual data show a good model fit (Appendix 2).

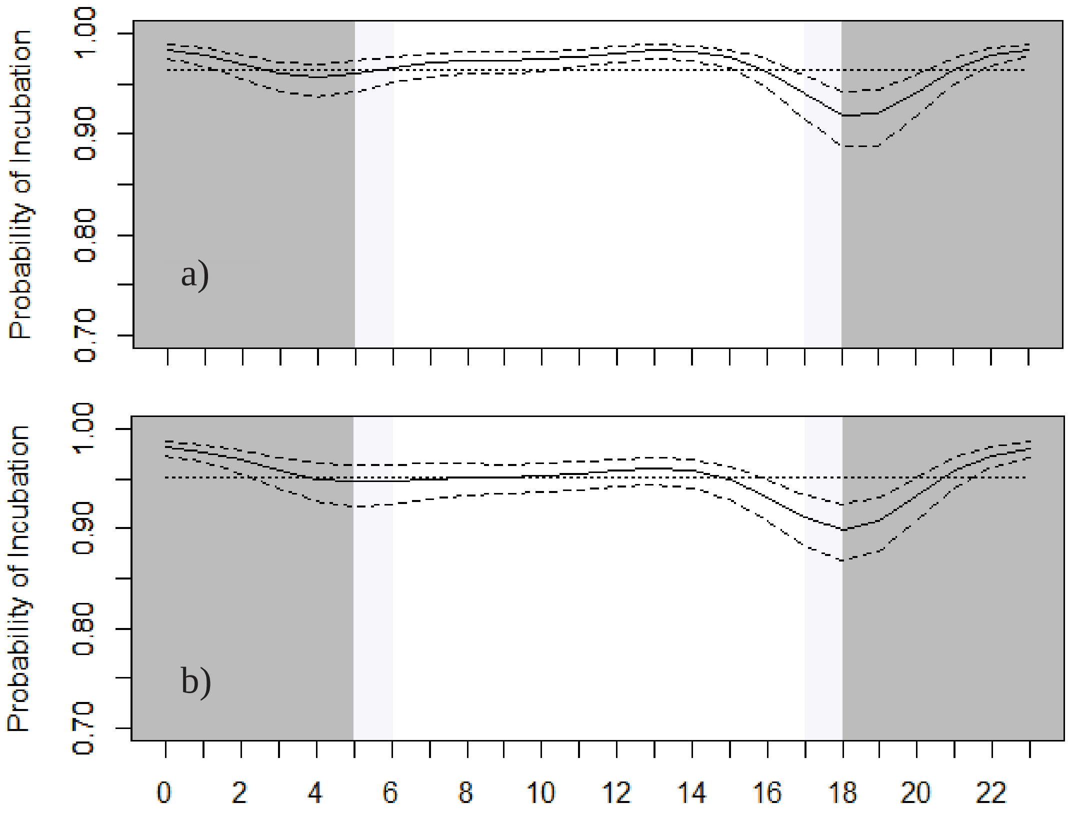

Figure 11: Prediction (solid line) and 95 % CI (dashed lines) for Black Skimmer incubation pattern across the diel period, a) for A2 model and b) for A3 model. The dotted horizontal line presents MESOR, calculated at 0.96 and 0.95 for A2 and A3 respectively. Note that the y-axis scale is scaled at 0.7 to 1. Parameter estimates for the respective best ranked GLMMs used for prediction and CI calculation are presented in Table 10.

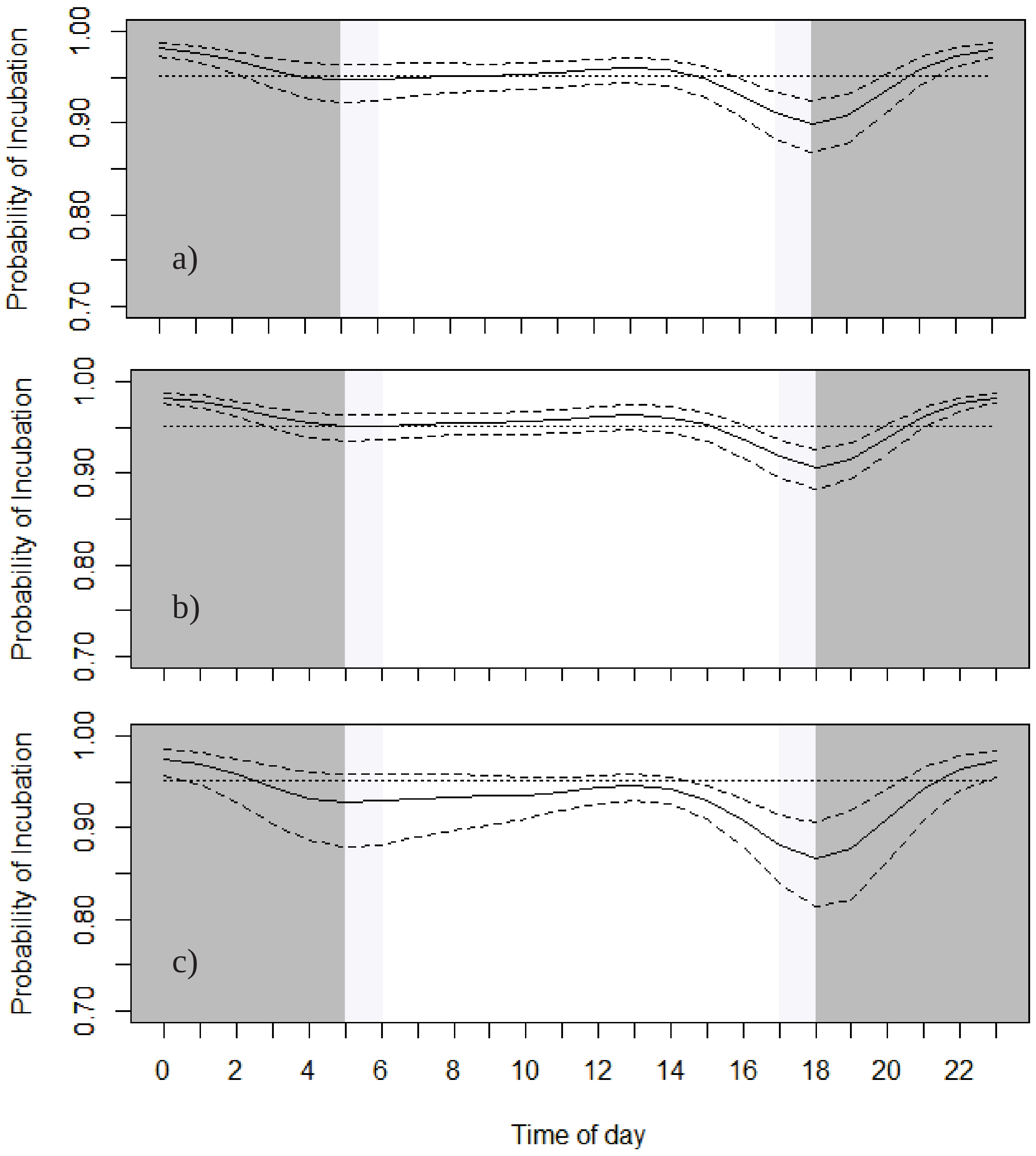

Figure 12: Diel pattern of incubation by Black Skimmers in A3, predicted at different ambient temperatures. Prediction (solid line) and 95 % CI (dashed lines) for a) min ambient temperature 19.1°C; b) mean ambient temperature 25.5°C; c) max ambient temperature 34.9°C. The dotted horizontal line presents MESOR. Note that the y-axis scale is scaled at 0.7 to 1. Parameter estimates for the best ranked GLMM used for prediction and CI calculation, are presented in Table 10.

Table 10: Parameter estimates of the most parsimonious GLMMs ≤ Δ2.0 AIC$_c$ of lowest ranking model, on which predictions are based. 'iii' refers to the set of cosinor functions as presented in section 2.5.4. Models are presented for each response and attempt. Random effects, their variance and SD are referred to in *italics*.

Attempt 2 models					**Attempt 3 models**				
Variable	**Estimate** */Variance*	**SE** */SD*	***P***	**ΔAIC$_c$**	**Variable**	**Estimate** */Variance*	**SE** */SD*	***P***	**ΔAIC$_c$**
Incubation ~ iii + Days until hatching + (1| Nest ID)				1.45	**Incubation ~ iii + Days until hatching + Ambient Temperature+ (1| Beach ID/Nest ID)**				0.00
(Intercept)	3.794	0.195	< 0.001		(Intercept)	5.445	0.517	< 0.001	
I(cos(2 * pi * Hour/24))	-0.116	0.044	0.008		I(cos(2 * pi * Hour/24))	0.273	0.097	0.005	
I(sin(2 * pi * Hour/24))	0.184	0.035	< 0.001		I(sin(2 * pi * Hour/24))	0.193	0.058	0.001	
I(cos(2 * 2 * pi * Hour/24))	0.551	0.039	< 0.001		I(cos(2 * 2 * pi * Hour/24))	0.506	0.051	< 0.001	
I(sin(2 * 2 * pi * Hour/24))	-0.006	0.038	0.881		I(sin(2 * 2 * pi * Hour/24))	-0.014	0.041	0.735	
I(cos(3 * 2 * pi * Hour/24))	0.181	0.038	< 0.001		I(cos(3 * 2 * pi * Hour/24))	0.136	0.036	< 0.001	
I(sin(3 * 2 * pi * Hour/24))	-0.273	0.039	< 0.001		I(sin(3 * 2 * pi * Hour/24))	-0.167	0.036	< 0.001	
Days until hatching	-0.036	0.007	< 0.001		Days until hatching	-0.104	0.007	< 0.001	
Nest ID	*0.281*	*0.530*			Ambient Temperature	-0.045	0.020	0.024	
					Nest ID: Beach ID	*0.103*	*0.321*		
					Beach ID	*0.000*	*0.000*		
Sleeping posture ~ iii + Days until hatching + Ambient Temperature + (1|Nest ID)				0.00	**Sleeping posture ~ iii + Days until hatching + Ambient Temperature + (1|Beach ID/ Nest ID)**				0.00
(Intercept)	3.124	0.276	< 0.001		(Intercept)	1.133	0.357	0.002	
I(cos(2 * pi * Hour/24))	-0.062	0.025	0.012		I(cos(2 * pi * Hour/24))	-0.163	0.051	0.001	
I(sin(2 * pi * Hour/24))	-0.637	0.037	< 0.001		I(sin(2 * pi * Hour/24))	0.133	0.032	< 0.001	
I(cos(2 * 2 * pi * Hour/24))	-0.037	0.017	0.025		I(cos(2 * 2 * pi * Hour/24))	-0.094	0.024	< 0.001	
I(sin(2 * 2 * pi * Hour/24))	0.242	0.020	< 0.001		I(sin(2 * 2 * pi * Hour/24))	-0.143	0.020	< 0.001	
I(cos(3 * 2 * pi * Hour/24))	0.555	0.016	< 0.001		I(cos(3 * 2 * pi * Hour/24))	0.546	0.0178	< 0.001	
I(sin(3 * 2 * pi * Hour/24))	-0.147	0.015	< 0.001		I(sin(3 * 2 * pi * Hour/24))	-0.303	0.018	< 0.001	
Days until hatching	-0.012	0.003	0.001		Days until hatching	0.012	0.005	0.008	

Ambient Temperature	-0.153	0.009	< 0.001		Ambient Temperature	-0.089	0.011	< 0.001	
Nest ID	*0.182*	*0.427*			*Nest ID: Beach ID*	*0.012*	*0.111*		
					Beach ID	*0.255*	*0.505*		
Prop. Male Incubation ~ iii + Days until hatching + (1|Nest ID)				0.00	**Prop. Male Incubation ~ Days until hatching + (1|Beach ID/ Nest ID)**				0.00
(Intercept)	-0.049	0.174	0.779		(Intercept)	0.002	0.224	0.993	
I(cos(2 * pi * Hour/24))	0.130	0.108	0.230		Days until hatching	-0.070	0.020	< 0.001	
I(sin(2 * pi * Hour/24))	0.173	0.108	0.109		*Nest ID: Beach ID*	*0*	*0*		
I(cos(2 * 2 * pi * Hour/24))	-0.066	0.109	0.545		*Beach ID*	*0*	*0*		
I(sin(2 * 2 * pi * Hour/24))	0.3440	0.107	0.001						
I(cos(3 * 2 * pi * Hour/24))	0.285	0.108	0.009						
I(sin(3 * 2 * pi * Hour/24))	-0.167	0.107	0.119						
Days until hatching	-0.046	0.015	0.003						
Nest ID	*0.002*	*0.047*							
Incubation bout length ~ iii + log10(Ambient Temperature) + Gender				0.00	Model fits were poor and much overdispersed. While the model with the same explanatory variables as the one presented for A2 had the lowest AIC$_c$ value, the model is not presented, as it possibly was unreliable.				
(Intercept)	7.829	1.005	< 0.001						
I(cos(2 * pi * Hour/24))	-0.024	0.056	0.674						
I(sin(2 * pi * Hour/24))	0.046	0.041	0.264						
I(cos(2 * 2 * pi * Hour/24))	0.026	0.033	0.432						
I(sin(2 * 2 * pi * Hour/24))	0.051	0.028	0.071						
I(cos(3 * 2 * pi * Hour/24))	0.105	0.027	< 0.001						
I(sin(3 * 2 * pi * Hour/24))	-0.076	0.027	0.005						
Log10(Ambient Temperature)	-3.403	0.726	< 0.001						
Gender	-0.234	0.038	< 0.001						
Nest ID	*0.047*	*0.218*							

Although, incubation was shared almost equally between genders, males incubated slightly less. Males were in 43% and 40% of images with an incubating bird, in the second (A2) and third breeding attempt (A3), respectively. Moreover, males were predicted to have slightly less than 0.5 proportion incubation across the day in A2, with periods of significantly lower proportion in the middle of the day and after dusk (Figure 13). Both for A2 and A3, proportion of male incubation is lowest at the start of the incubation period and is predicted to increase as the period progresses (Table 10; Figure 14).

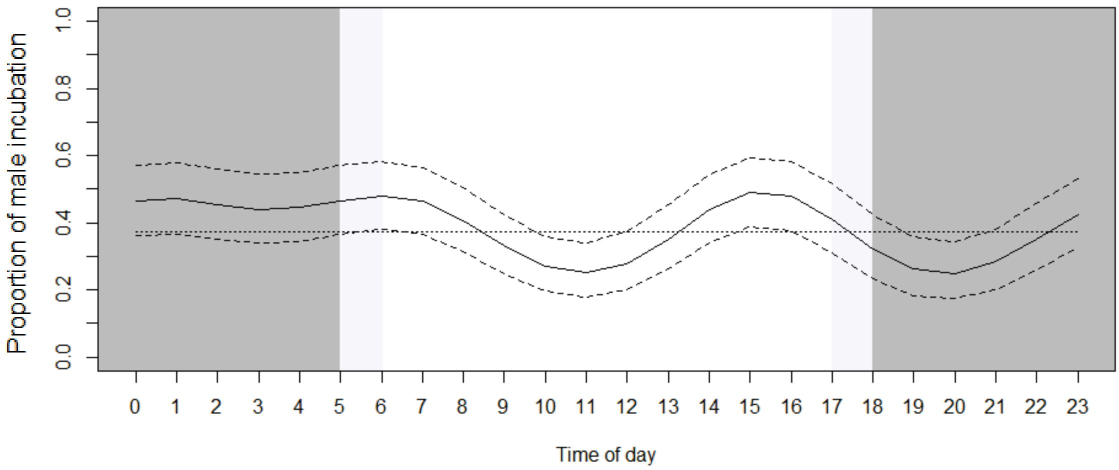

Figure 13: Diel pattern of incubation carried out by male Black Skimmers in A2. Prediction presented by solid line and 95 % CI as dashed lines. MESOR is calculated at 0.37 and shown by the horizontal dotted line. Parameter estimates for the best ranked GLMM used for prediction and CI calculation, are presented in Table 10.

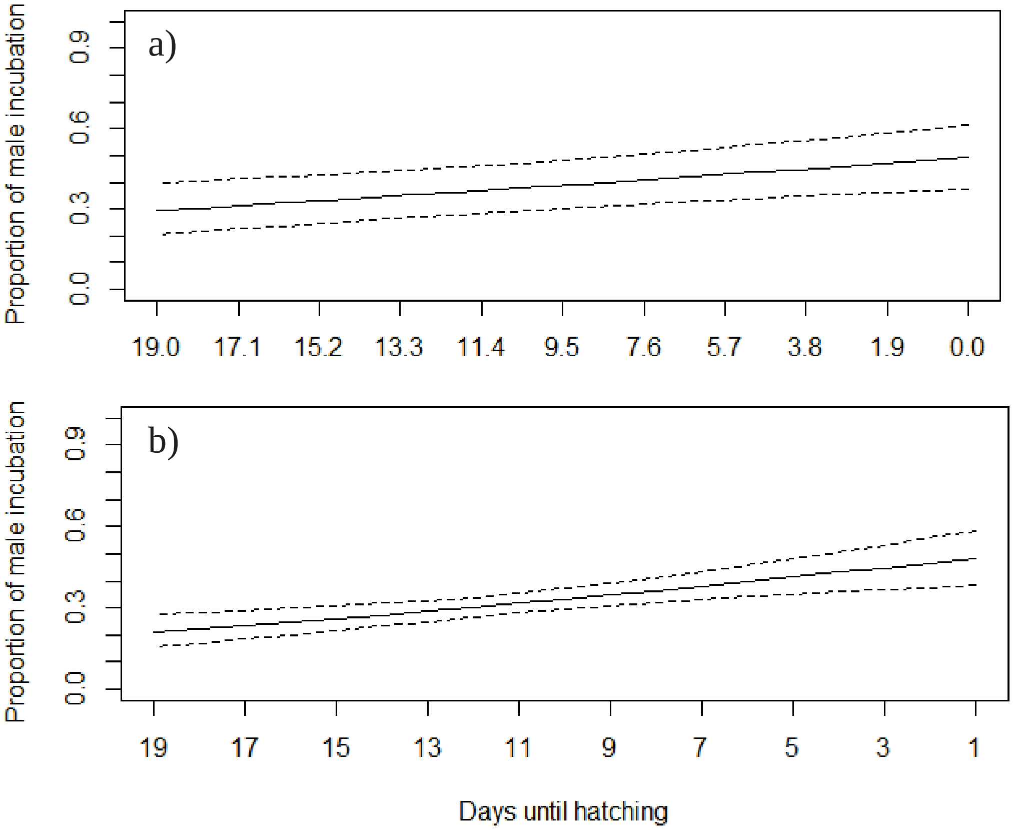

Figure 14: Proportion of male Black Skimmer incubation predicted (solid line) against days until hatching for A2 (a) and A3 (b). Dashed lines present 95 % CI. Parameter estimates for the respective best ranked GLMMs used for prediction and CI calculation, are presented in Table 10.

Probability of sleeping posture decreases significantly before dawn and after dusk in both A2 and A3 (Figure 15). In A3, it also decreases significantly in the middle of the day (Figure 15), at the same time when a peak is observed in the mutually exclusive extended neck behaviour (Figure 16). Moreover, sleeping posture was predicted to decrease with increasing ambient temperature for both A2 and A3 (Table 10), but with a larger parameter estimate in A2 (Table 10; Figure 17).

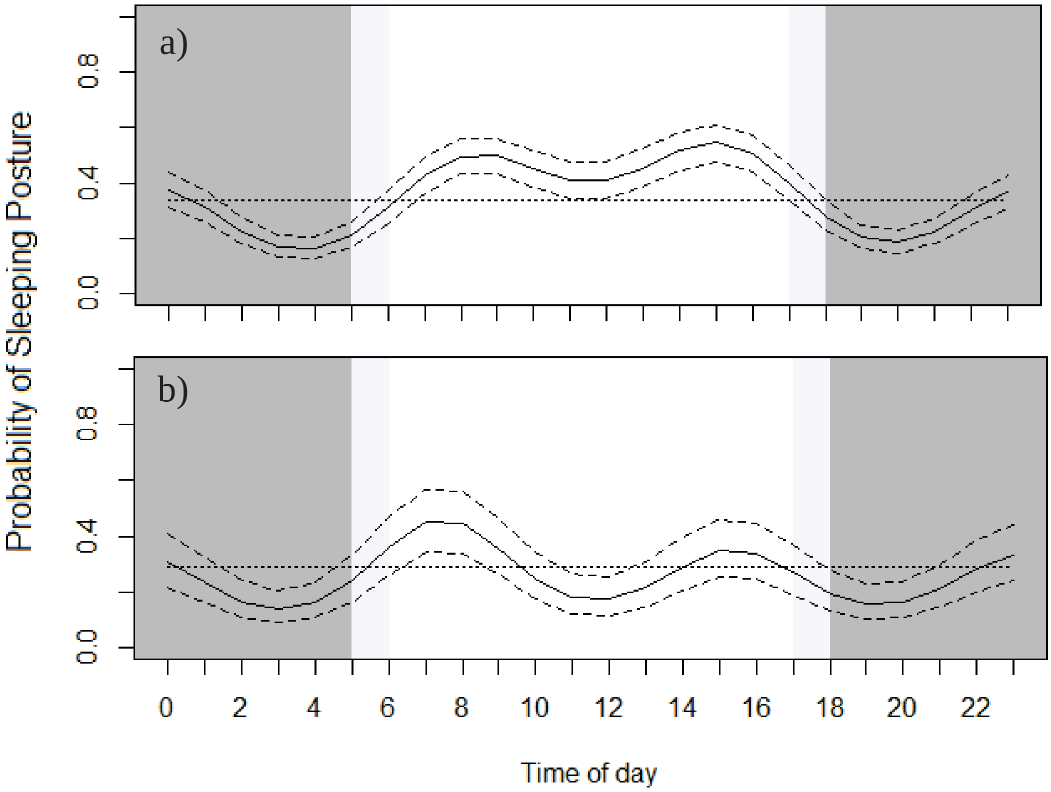

Figure 15: Probability of sleeping posture in Black Skimmers across the diel period, for (a) A2 and (b) A3 as predicted (solid line) by the respective best ranked GLMM models (Table 10). 95% CI shown by dashed lines, MESOR by the horizontal dotted line.

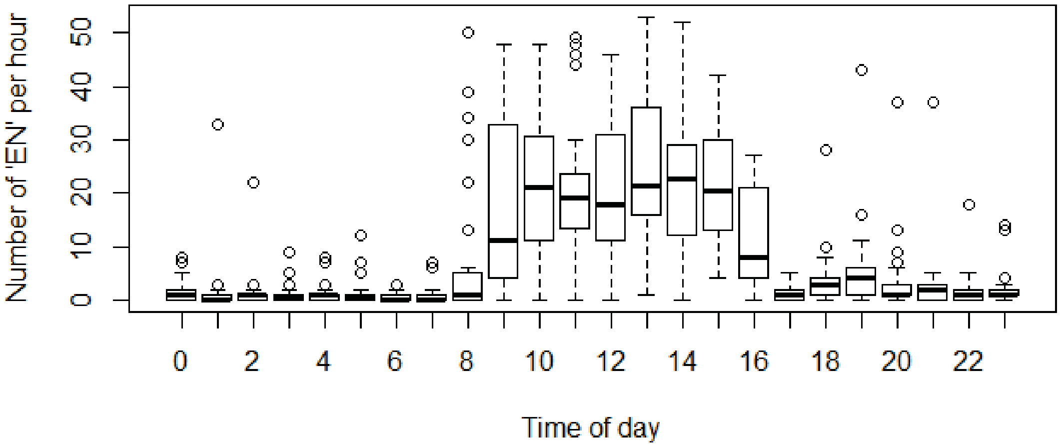

Figure 16: Extended neck behaviour, a proxy for heat dissipating mechanisms, in incubating Black Skimmers given as a count per hour in the third attempt, A3.

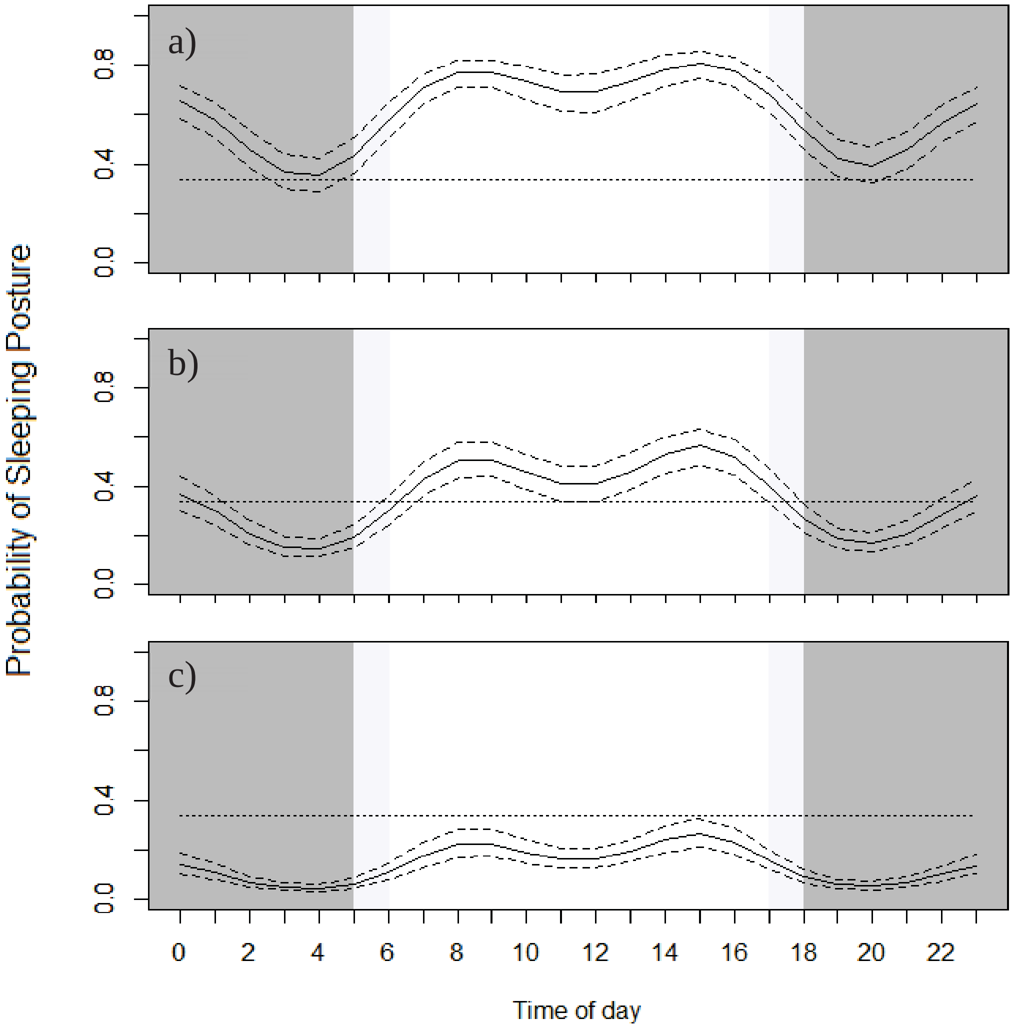

Figure 17: Sleeping posture diel patterns in Black Skimmers, predicted (solid line) and 95 % CI (dashed lines) for A2 at a) min ambient temperature 16.6°C; b) mean ambient temperature 24.3°C; c) max ambient temperature 32.7°C. MESOR is shown by the dotted horizontal line in each case. Parameter estimates for the best ranked GLMM used for prediction and CI calculation, are presented in Table 10.

Incubation bout length was a mean of 20.55 mins (±17.60 SD) and 17.08 mins (±17.37 SD) in A2 and A3, respectively. The longest bout recorded was 150 mins. The predicted diel pattern of incubation bout length for A2, was rather constant and 95 % CI overlap MESOR throughout (Figure 18). However, incubation bout length decreased with increasing ambient temperature according to model predictions (Table 10; Figure 19). Furthermore, females were predicted to incubate in longer bouts than males (Table 10), with an indication of longer bouts even with increasing ambient temperatures (Figure 20).

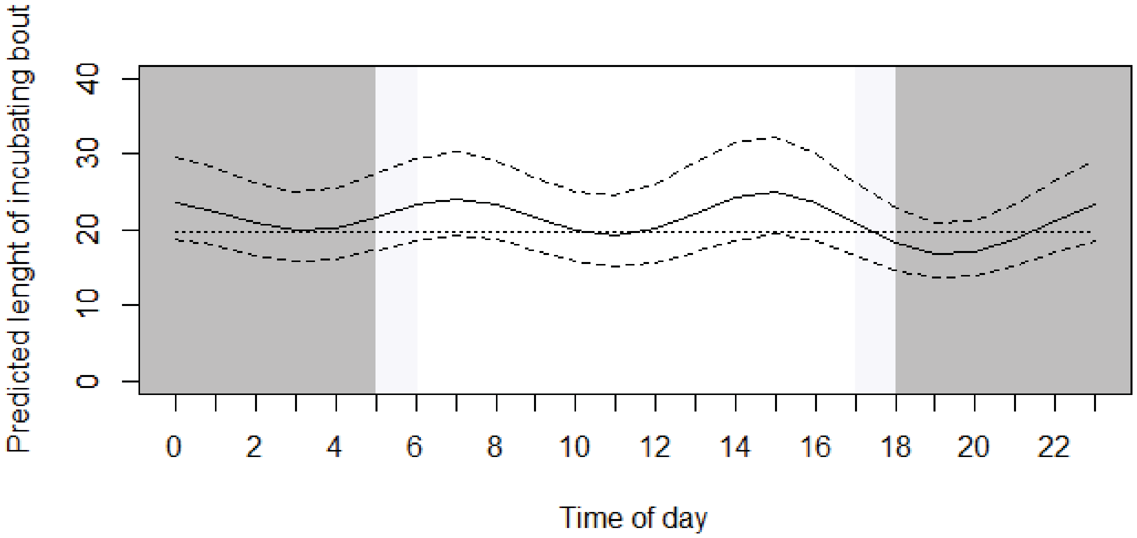

Figure 18: Predicted diel pattern (solid line) of Black Skimmer incubation bout length for A2. 95% CI shown by dashed lines, MESOR by the horizontal dotted line. Parameter estimates for the best ranked GLMM used for prediction and CI calculation, are presented in Table 10.

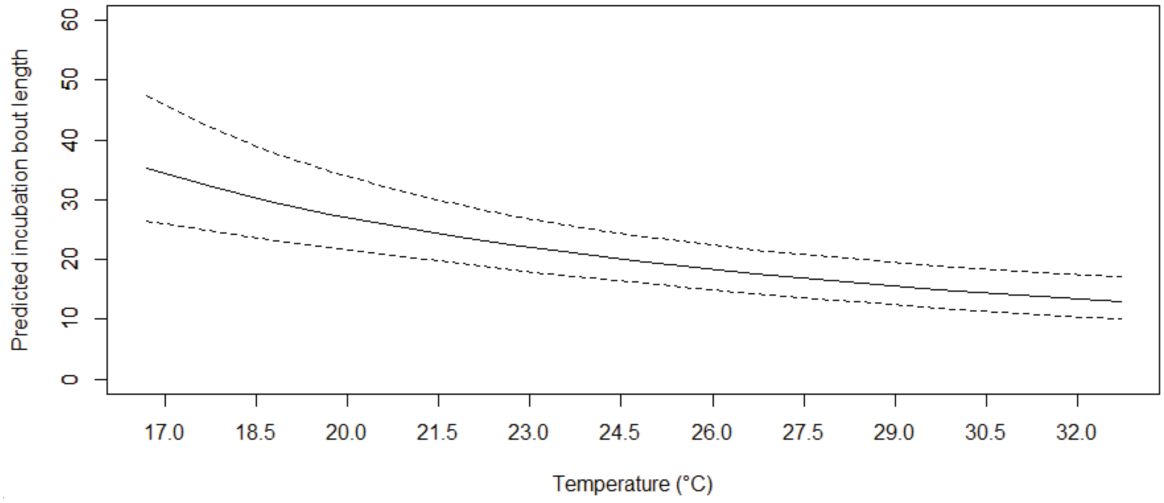

Figure 19: Prediction (solid line) and 95 % CI (dashed lines) for incubation bout length by Black Skimmers in A2, as explained by ambient temperature. Parameter estimates for the best ranked GLMM used for prediction and CI calculation, are presented in Table 10.

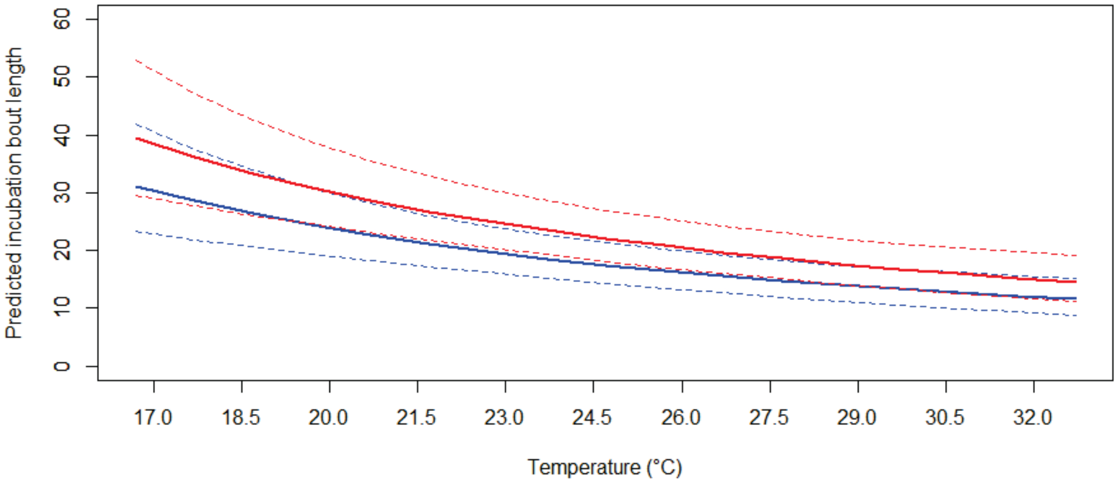

Figure 20: Prediction of incubation bout length against ambient temperature, for female Black Skimmers (red solid lines) and for males (blue). Dashed lines in respective colours present 95 % CI. Parameter estimates for the best ranked GLMM used for prediction and CI calculation, are presented in Table 10.

3.6 Nest Outcome

Flooding was the main reason for nest failure in the first (A1) and second nesting attempts (A2) (Figure 21). Eggs hatched in five of the 23 nests in A2, but were flooded shortly after and nestlings did not survive. A smaller flood during A3 only destroyed one nest, which was the one closest to the river. Predation accounted for five nest failures (Figure 21). Four predator species were recorded on camera trap images. Ocelot (*Leopardus pardalis*) was the only mammal predator recorded and was responsible for the predation of one nest. Black Caracaras (*Daptrius ater)* and a Black Vulture (*Coragyps atratus*) together predated another nest, while two Great Black Hawks (*Buteogallus urubitinga*) predated a third. A fourth predated nest was surrounded by bird of prey tracks in the sand, while the predator of the fifth remains unknown. Six nests were successful in A3 (Figure 21). Nestlings from these nests were followed until the end of the study period, when they had reached around 15 days of age, but had not yet fledged.

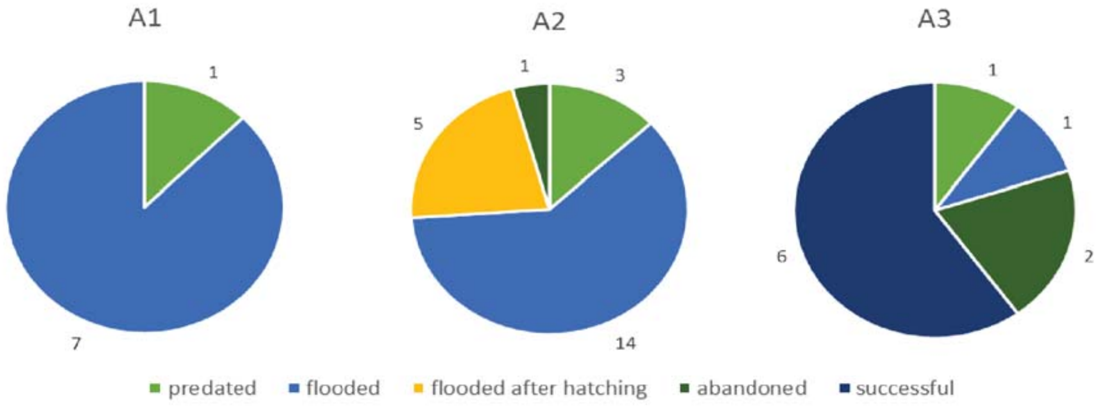

Figure 21: Outcomes of the nests in A1 (29th June – 08th July), A2 (13th July – 9th August) and A3 (19th August – 30th September). Nests that were not visited in the hatching and nestling period and thus with unknown outcome were not included. While five of the nests in A2 did hatch, the nestlings were flooded shortly after. In the 'successful' nests in A3 nestlings were followed to around 15 days of age but the fieldwork ended before they reached fledging.

4. Discussion

4.1 Beach Choice and Nest site selection

46 % of the beaches in the study area were used at least once by nesting Black Skimmers. The distribution sustains the suggestion by Zarza et al. (2013), that active selection choices are made between beaches with different abiotic charactersitics. Moreover it is the same beach-use proportion as that recorded in a more complete survey of River Manu in 1987, incorporating 81 beaches rather than 35 beaches in this study (Groom 2013). This might indicate that the Manu population is stable. Although the maximum number of pairs recorded per beach was less in this study, it cannot be discounted that there were larger concentrations on the non-sureveyed beaches.

4.1.1 Social aggregation and distance to oxbow lakes

The most important habitat factor that positively influenced beach selection was beach width. The distance to the closest beach having been used by nesting Black Skimmers, was also present as an explanatory variable in beach choice models with lowest AIC_c value. The positive estimates should not necessarily be interpreted as probability of beach selection increasing with distance from beaches with other nesting Black Skimmers, especially when the variable is non-significant. An alternative explanation is likely to the positive estimates. The wider beaches, which Black Skimmers are shown to select, were not necessarily close to each other. In fact several smaller beaches were located between the larger ones. Therefore, the arrangement of beaches along the narrow Manu River might hinder social attraction of nesting Black Skimmers. In contrast, in the Anavilhanas Archipelago in the the Brazilian Amazon, Black Skimmers nesting was more likely close to the two main colonies present (Zarza et al. 2013). Social attraction might have been possible in the wider river, with beaches found close to each other. Furthermore, the Anavilhanas study covered a larger area (Zarza et al. 2013) than this study, possibly allowing for better detection of social attraction trends.

The small scale of the study area may also have been the reason for lack of detection of any trends in distance to oxbow lakes from nesting beaches. Satellite telemetry of Black Skimmers during the breeding season at the Manu River revealed movements of several hundred kilometres to and from other watersheds and wetlands, indicating how easily the species can move over large distances. (Davenport et al. 2016). Nonetheless it is unknown for what purpose the birds moved so far during the breeding season, and whether they had active nests.

4.1.2 Beach fidelity

All nests were unsuccessful in the first two attempts in this study, allowing for testing site re-use within one season. Re-nesting occurred on ten of sixteen beaches. The probability of beach re-use was affected positively by beach width. Strong preference to specific beaches due to abiotic factors could be one reason for high intra-season re-use. This explanation would hold true even if it was not the same pairs re-nesting on the beach. Another study from the Manu River recorded high beach re-use by Black

Skimmers between two consecutive years (Groom 2013). Individual site fidelity has also been recorded on the Manu River, with one colour-ringed female having bred on the same beach where it was tagged two years earlier (Davenport et al. 2016). Further evidence for individual site fidelity was gathered in this study, three colour-ringed birds having nested on the same beach for consecutive attempts. This contrasts with the theory that beach fidelity of Black Skimmers in the Amazon should be low and colonisation opportunistic (Gochfeld 1978), based on the hypothesis that site fidelity requires stable habitat (e.g. McNicholl 1975). The sandy beaches on which Black Skimmers breed in parts of the Amazon are in fact dynamic and can change between years (Raeder & Bernhard 2003). However, this might be different for the Manu River, where Robinson & Terborgh (1997) indicate that rate of meander position change is on the scale of decades for at least parts of the river.

Additionally, the main reason of nest failure in this study was flooding, which might be an unpredictable risk and does not stimulate site abandonment. On the Atlantic coast of the United States, a five year study revealed that Black Skimmer colonies often re-used sites where flooding had destroyed nests, but did not nest again at sites with high predation rates (Burger 1982). Moreover, the two large floods in the study period that covered entire beaches may not allow for natural selection to act in favour of birds nesting in less flood prone sites higher on the beach. In light of these findings, continuous monitoring of river level and floods is suggested as well as further tagging of Black Skimmers to provide more data on individual site fidelity. Recording reason for nest failure and whether abandonment occurs by the respective pairs or colonies, would allow for an Amazonian counterpart to the study by Burger (1982) if carried out over several seasons.

4.1.3 Colony size and density on beaches

The number of nests per beach in the study area was low. A maximum of six Black Skimmer pairs were recorded nesting on the same beach, while single pairs were more common. Groom (2013) documented 1 to 12 pairs per occupied beach on the Manu River, for 81 beaches surveyed in 1987 and 1988. Slightly larger densities are reported from the Anavilhanas Archipelago (Zarza et al. 2013). Nevertheless, densities found on the Manu River and Anavilhanas Archipelago contrast to the higher concentrations registered at single colonies on the Trombetas River (Krannitz 1989) and Solimões Rivers (Raeder 2003), both in the Brazilian Amazon. While the beaches are larger than the ones in Manu, distance between nests found in this study (section 3.2) are larger than distances reported from the Trombetas and Solimões Rivers. Anthropogenic disturbance including frequent egg harvesting as well as cattle farming on other available beaches, has been recognised as the probable reason for the dense colonies of Black Skimmer at the Solimões study site (Raeder 2003; Zarza et al. 2013). Black Skimmers in much of the United States coast, also aggregate at the remaining available sites not yet completely occupied by humans (Burger 1982; Dinsmore 2008; Gochfeld 1978; Gordon et al. 2000). Nesting in dense colonies has some positive effects such as a highly reduced predation rate (Burger 1981a; Groom 1992; Raeder 2003). On the other hand, there are several negative effects of breeding in dense colonies. The most noteworthy is perhaps aggression between neighbouring adults and even fatal attacks on nestlings of other pairs (Burger 1981a; Quinn et al. 1994; Raeder 2003). The lower densities of Black Skimmers found in the Manu River might indicate more natural distributions in the lack of human influence, as has also been suggested for the protected Anavilhanas Archipelago (Zarza et al. 2013).

Further studies are necessary to distinguish between habitat suitability for Black Skimmers across different Amazonian rivers, in terms of nesting sites, food abundance and anthropogenic influence. In this study, I made an attempt at recording feeding rate of nestlings by adults. However, in contrast to what is reported in literature (Groom 1992), no feeding of young was observed during the day (pers. obs.). Since feeding of young was observed to start just before dusk and continued into rapidly failing light conditions, any adequate study of foraging and feeding rates by Black Skimmers in the Amazon is suggested to utilise night vision equipment. Timing of foraging depends on fish prey species present (Willard 1985), as well as the type of water bodies, creating a mixture of conclusions on the patterns of foraging by Black Skimmers. For example, from a coastal study site in the United States, tides appear to have a larger influence on foraging than time of day (Erwin 1977), while at an inland lake in California no diurnal feeding of young was observed (Grant and Hogg 1976). From yet another coastal site in the United States, diurnal feeding was observed, but the rate was doubled at night (Gordon et al. 2000).

4.1.4 Beach selection as function of predation risk reduction?

Most Black Skimmers selected nest sites far away from vegetation and none right next to vegetation, findings also shown by Groom (2013). In light of this, the higher probability of nesting on wider beaches, might be due to preference to nest placement as far away as possible from the vegetated beach rear. Wider beaches allow for greater distance between nests and beach rear. On beach islands in the Anavilhanas, Black Skimmers selected islands further away from river margins that were vegetated (Zarza et al. 2013). Birds placing nests further away from vegetated margins, has been attributed to reduced nest predation and easier predator detection (Davenport et al. 2016; Grant 1982; Groom 2013, Zarza et al. 2013). Groom (2013), showed that there was a higher probability of nest predation closer to the vegetated beach rear, both for artificial nests and real nests.

However, it is not only nest predation that is a risk, but attacks on the adults themselves when at the nest. Two attacks on nest attending Black Skimmers are recorded from the Manu River. The predators were Roadside Hawk (*Buteo magnirostris*; Davenport et al. 2016) and Jaguar (*Panthera onca*; Groom 2013). While the predation rate might be low, theory would suggest that birds with relatively long life spans and low annual productivity would respond strongly to avoid even low adult predation risks (Amat & Masero 2004a; Ghalambor & Martin 2001; Tieleman et al. 2008). In other shore nesting birds, several pairs choose open areas to avoid the much higher adult predation rate close to vegetation, even though thermal stress to both eggs and adults could be drastically reduced by breeding in vegetation cover (Amat & Masero 2004a; Lomas et al. 2014). A similar trend was found in desert breeding Hoopoe Larks

(*Alaemon alaudipes*), choosing open nesting sites early in the season most likely to reduce adult predation risk, while preference shifted to cover as temperatures increased further with season (Tieleman et al. 2008).

4.1.5 Thermal regulation by nesting close to river?

In nesting further away from the vegetated beach rear, Black Skimmers consequently also place nests close to the river edge both in terms of distance and height (Table 8; Groom 2013; Krannitz 1989). It has been suggested that the proximity to the river reduces the sand temperature in the nests, even though flood risk is increased (Davenport et al. 2016). A small-scale test of this thermal regulation hypothesis, showed that temperature range recorded at the beach surface was significantly lower closer to the river edge (Table 9; Figure 8). However, adjusted R^2 (0.57 and 0.49 for models with height and distance explanatory variables respectively) was rather low. Furthermore, to what extent Black Skimmer nests benefit from this trend is not yet clear and therefore there is further room for testing of this hypothesis. Groom (2013) documents a slightly higher hatching success of nests at lower beach height in a year without flood loss, but whether this is related to benefits from thermal regulation by the river is not clear.

Additionally, the tendency to nest close to the river edge may be linked to shorter distance when flying to the river to wet the feet and ventral feathers. This behaviour, known as 'foot-wetting' or 'belly-soaking', is an adaptation to heat stress in some shore nesting birds, intended to reduce overheating for both the incubating birds and eggs (Grant 1982). It is frequently observed in Black Skimmers (Grant & Hogg 1976; Groom 2013; pers. obs.). Longer flight distances between nests and water would decrease the efficiency of cooling for the adults since flight produces body heat (Amat & Masero 2004b). Western Gull (*Larus occidentalis*) appear to breed as close to the sea as possible in the Gulf of California, allowing for short flight distances to bathe and thus also minimal time when nests are exposed between bouts (Hand et al. 1981). Furthermore, Kentish Plovers (*Charadrius alexandrinus*) breeding on lake shores were more successful closer to the water, attributed to the ability to belly-soak more frequently than pairs further away, and thus being able to attend nests more continuously on hot days (Amat & Masero 2004b).

4.2 Nest Temperature and Incubation behaviour

4.2.1 Nest Temperature

The presence of incubating birds on the nest during the day prevents nest temperatures to increase as much as temperatures on the sand surface. This confirms the hypothesis that despite (extreme) diel temperature fluctuations on the sandy beaches, nest temperatures were kept more constant. The fact that incubation can have a cooling role during parts of the diel cycle contrasts to the general perception of incubation (Deeming 2002), but is actually common for birds that breed in hot environments, requiring several behavioural adaptations by incubating adults (Alrashidi et al. 2010; Grant 1982; Walsberg & Voss-Roberts 1983; Ward 1990).

Nevertheless, nest temperatures documented in this study should not be interpreted as temperature experienced by the eggs. *i*Buttons® were placed at the bottom of the nest, underneath the eggs, and were therefore not in contact with the brood patch of the incubating bird or exposed to direct sunlight when eggs were uncovered. Moreover, although the *i*Buttons® were secured on top of long nails inserted in the substrate below the nest, position still varied slightly as incubating birds shifted sand around in the scrape. Shifting of the loggers themselves or nesting material around them is a readily faced problem when utilising *i*Buttons® in nests (Bayard & Elphick 2011; Smith et al. 2015; Schneider & McWilliams 2007). However, there is a significant difference between temperature ranges between active and abandoned nests with the same number of eggs and *i*Button® setup. This indicates that the narrower temperature range observed in active nests is truly an effect of incubation rather than position of the *i*Buttons®, and the abovementioned limitations have little effect on the interpretations made.

4.2.2 Constant Incubation

Black Skimmers incubate almost constantly, probably to keep the nest temperature within the demonstrated range. MESOR, indicating mean diel incubation activity, was very high, 0.96 and 0.95 in attempt two and three respectively. The highest incubation probability occurred at night between 22PM and 3AM. At this time incubation had a warming effect shown by higher nest temperatures than the beach surface temperatures. Fatal damage by overcooling is unlikely in the tropics, but in the absence of incubation embryo development might be greatly reduced (Conway & Martin 2000; Webb 1987). Furthermore, Black Skimmers defend nests actively (Burger 1981b; Groom 1992), and therefore they might maintain high incubation constancy not only for nest temperature control but also for anti-predatory reasons. In Arctic shorebirds it was shown that length of time without an incubating bird at the nest was positively associated with egg predation, probably due to less immediate nest defence (Smith et al. 2012).

On the other hand, incubation probability decreased at around 17 to 19hrs. This coincides with dusk and the first hour of darkness as well as a visible overlap in beach surface and nest temperatures. Dusk seems to be an important time for Black Skimmers to forage (Grant & Hogg 1976; pers. obs.), coinciding with a period where regulation of nest temperature might be less important. The pattern of decreased incubation in the part of the day with most efficient foraging opportunities, has also been observed in the piscivorous Arctic Tern (*Sterna paradisaea*) (Skipnes 1983).

As shown in this study, constancy of incubation is expected to be kept high throughout the nesting attempt for species with biparental care (Deeming 2002; Marasco & Spencer 2015). Additionally, incubation was increased slightly closer to hatching. This could be an effect of incubating birds attempting to regulate nest temperatures more closely, due to older embryos possibly having narrower thermal tolerances (Webb 1987). Additionally, higher incubation effort could also be an effect of increased value of the eggs with the level of investment already put into the nesting attempt, as well as the eggs' higher chance of hatching (Andersson et al. 1980; Montgomerie & Weatherhead 1988).

4.2.3 Thermal regulation in incubating adults

Findings are in line with the hypothesis made that incubating Black Skimmers regulate nest microclimate in high temperatures at the expense of thermal stress to themselves. Incubation bout length decreased with increasing ambient temperature. Probability of incubation also decreased slightly with higher temperatures, albeit without significant changes to the diel incubation pattern. These indicate a change in incubation strategy by Black Skimmers at higher temperatures. During the high daytime temperatures the risk of embryo damage is greatest, and birds incubating in hot environments have to achieve a balance between preventing overheating of themselves and of the eggs (Alrashidi et al. 2010; Amat & Masero 2004b; Bartholomew & Dawson 1979; Webb 1987). Flying to the river to wet ventral parts of the body as a cooling mechanism may be crucial do prevent overheating. The shorter incubation bouts shown here are therefore probably caused by the need to leave the nest for river bathing. A trend of shorter incubation bouts at higher temperature is documented in other ground nesting species that use water bodies for cooling (Alrashidi et al. 2010; Amat & Masero 2004b; Grant 1982; Purdue 1976; Williams et al. 1989).

Black Skimmers resort to behavioural cooling mechanisms while at the nest as well, which by using the extended neck behaviour as an indicator are shown to peak in the middle of the day. The mechanisms are primarily aimed at increasing convective heat loss and decreasing heat gain from solar radiation and include gaping, raising dorsal feathers (ptiloerection) and displacing wings outwards in a drooping position (Grant & Hogg 1976). Depending on the orientation of the incubating bird, some of the abovementioned mechanisms were difficult to note separately in camera trap images. Nevertheless, the category 'extended neck' (Figure 5a & b), was often associated with gaping, ptiloerection and drooping wings and can therefore, be used as a proxy for heat dissipating mechanisms. An extended neck when panting and erecting dorsal feathers has also been recorded elsewhere for Black Skimmers (Grant & Hogg 1976), as well as in incubating gulls (Bartholomew & Dawson 1979). However, incubating birds sometimes extend their neck as they become more alert, especially at night.

Ptiloerection on the black coloured backs and crown of skimmers might be particularly effective. Elevated black plumage has been shown to gain less heat at wind speeds of 3m/s or more, compared to white plumage, although the opposite is true in the absence of wind (Walsberg et al. 1978). In light of this, it would be interesting to investigate the responses of incubating Black Skimmers to different wind speed on beaches. River breezes, created by the differences in the river water and land temperatures during the day, have been recorded to affect climate circulation in eastern Amazonia (Pereira de Oliveira & Fitzjarrald 1993; Silva Dias et al. 2004). While air circulation along narrower rivers like the Manu

River might not be enough to affect larger scale climate patterns, it could be of significant cooling advantage for incubating birds on beaches.

On the other hand, when the Black Skimmers laid their head and beak in on or between the back feathers in a sleeping posture, the abovementioned cooling mechanisms are not carried out. The sleeping posture decreases with increasing ambient temperature, and for A3 it also decreases significantly in the middle of the day. Similarly, the same sleep posture as seen in the skimmers, is not performed by gulls during hot temperatures (Amlaner & Ball 1983). The posture seems to decrease body heat loss and is most evident in desert nesting Heermann's Gulls (*Larus heermanni*) during cooler periods of the day, (Bartholomew & Dawson 1979), in similarity to findings here. Nevertheless, whether the posture primarily has a sleeping or thermoregulatory function in birds is not yet clear (Reebs 1986; Javůrková et al. 2011; Wellmann & Downs 2009).

The decrease in the recorded sleeping posture before dawn and after dusk might contrast to a thermal regulatory function, but could have several explanations. Sleeping postures might be negatively correlated to time of day when feeding is most efficient, as well as periods with perceived higher predation risk (Amlaner & Ball 1983; Javůrková et al. 2011; Lima et al. 2005). Higher frequency of an attentive posture, rather than a sleeping posture, during the diel period most adequate for foraging has been shown in incubating Arctic Terns (Skipnes 1983). Finally, it cannot be excluded that incubating birds slept in other postures not easily detected from camera trap images, as there are other less obvious sleeping postures in birds (Amlaner & Ball 1983).

4.2.2 Biparental incubation

Black Skimmer pairs shared incubation almost equally, with a slightly larger effort by females. This contrasts to the hypothesis made that males would share a larger proportion of incubation than females on the Manu River. The hypothesis was based on findings from the United States, where it was suggested that higher predation pressure caused a larger proportion of nest attendance by males recorded in some colonies (Burger 1981a, Quinn 1990). While predation events recorded along the Manu river in this study were relatively few, Groom (2013) recorded high Black Skimmer nest failure in 1988. Due to the limited field of view of camera traps used, it was only possible to investigate the effort Black Skimmer adults put into incubation. For example, the role males and females played in nest defence could not be reliably observed. Both sexes have been shown to be involved in nest defence, but involvement changed with breeding stage (Burger 1981b). For example, males defended nest territories more during egg-laying and early incubation, probably to prevent the female mating with conspecific males (Burger 1981a). Relief from this need after the egg fertilization stage, might have caused the observed increase in incubation by males as incubation period progressed.

Changing proportions of male and female incubation while total nest attentiveness is kept high, support theory that in biparental systems parents compensate for changes in the effort made by the mate

(McNamara et al. 1999). It is also in line with suggestions that biparental incubation might be essential for successful breeding in extreme environments, where the need for both constant nest attentiveness and adult bird self-maintenance is high (Alrashidi et al. 2010; Bulla et al. 2014; DuRant et al. 2013). However, Black Skimmer males shared even less of the incubation at midday, when temperatures were highest. This constrasts with the hypothesis made that cooperation would be highest in periods of potential thermal stress. For example, Kentish Plovers were found to share incubation most equally during the hottest part of the day (Alrashidi et al. 2010). The combined findings of lower proportion Black Skimmer male incubation at midday and a slight indication of shorter incubation bouts even at higher ambient temperatures, might suggest that males pay a higher cost when incubating at such temperatures and that females are better adapted to incubate at higher temperatures. The smaller size of female Black Skimmers should mean that they are able to cool down more quickly and therefore able to return to the nest after shorter recesses, as seen in a comparison of plovers with different body sizes (Ward 1990). On the other hand, smaller birds gain heat more quickly than larger ones, but this is under the assumption that plumage mass and depth also decrease with size (Walsberg et al. 1978), which is not necessarily the case for female Black Skimmers. Further research on the differences in heat gain by male and female Black Skimmers, could thus shed further light on the possibility that size difference allows for pairs to incubate successfully at varying temperatures. Different thermoregulatory needs, has been suggested as a factor in the development of sexual size dimporphism in other taxa (Blanckenhorn 2005).

Finally, even though male Black Skimmers incubated less than their mates, they contributed to some extent throughout the day. This contrasts to other biparental systems that have been studied, where the sexes incubate predominantly for a large part of the diel cycle but noteably less in the rest (Alrashidi et al. 2010; Bulla et al. 2014; Kosztolanyi et al. 2009). Higher exchange rates between males and females at the nest shown in Black Skimmers is probably regulated by thermal stress during the day and more optimal foraging during at least parts of the night. However, the specific cues the birds used to decide when to replace a partner cannot be determined with data gathered. The frequent exchanges between incubating Black Skimmers make it suitable species for observing what cues are used in negotiating incubation effort and how quickly birds react to these.

4.3 Future prospects of the Black Skimmer population in Amazonia

The findings of this study have shown that nest sites selected by Black Skimmers are vulnerable to flooding. Predator avoidance and possibly thermoregulatory benefits seem to favour nest sites close to the river both in terms of distance and height. Black Skimmers may have adapted to flash floods by rapidly re-nesting after nest failure. However, taken the large number of nests destroyed by unpredictable flooding along the Manu River in this study and in 1987 (Groom 2013), further research could be carried out over multiple years to determine the frequency of such floods and effects on fledging success. Ultimately, whether the Manu River acts as a sink habitat, at least in some years could be determined with additional data on mortality and dispersal.

The entire Amazon region is seeing a rapid increase in hydroelectric power investment, disrupting natural river flow and trapping sediments (Junk 2013). This might be a new potential cause of nest flooding with sudden release of water from dams in the dry season. Further, if floodplain inundation during the wet season is reduced this might lead to more permanent vegetation growing on beaches, which in natural rivers is washed away (Terborgh 1985). While water release from dams has been proposed to match the natural patterns of water fluctuations, this might not be economically viable (Junk 2013). Inundation of nesting habitat by the reservoirs, as well as highly unpredictable water flows downstream of dams negatively affecting nest success, have already been shown for the African Skimmer (*Rynchops flavirostris;* Coppinger et al. 1988). Moreover, the availability of wide beaches has shown to be important for nesting of Black Skimmers. Trapping of sediments by dams could eventually effect downstream beaches when erosion exceeds deposition (Manyari & de Carvalho 2007).

Finally, this study has shown that Black Skimmers nesting on open and hot beaches seem to be adapted to the temperature extremes during incubation. Nevertheless, temperatures are predicted to rise in the Amazon region (Junk 2013). There is the need for further research on how close tropical species are to their thermal limits, and at what temperature incubating birds will be restricted in attending nests at the adequate constancy due to an increased need for self-maintenance behaviour, such as bathing (Oswald & Arnold 2012; Mainwaring 2015).

5. Conclusion

This study found evidence for Black Skimmers actively selecting between different beaches for nesting along the Manu River in the Peruvian Amazon. Wider beaches were preferred, probably driven by predation risk avoidance. Moreover, temperature range on the beach surface was shown to increase with distance and height from the river. However, to what extent nest microclimate is affected by this is still unclear, although Black Skimmers generally nested closer to the river. Nests are vulnerable to flash floods, which caused complete nest failure twice throughout the study area. This allowed for studying re-use of beaches within one nesting season, which was significantly dominated by attraction to the same beaches that were widest.

The nest-site selection of Black Skimmers on open beaches far from vegetation exposes nests and incubating birds to high daytime temperatures. However, nest temperatures were kept cooler than the beach surface through almost constant incubation. Biparental care is likely to be crucial in this respect, allowing adults to frequently replace each other at the nest and shorten incubation bouts. Birds still showed signs of behavioural heat dissipating mechanisms when incubating in the middle of the day. These were replaced by a heat conserving sleeping posture at cooler temperatures. Pairs shared incubation almost equally, with a slightly higher proportion of female incubation which was largest in the middle of the day. There was also an indication that females might incubate for longer bouts than males, even at higher temperatures. These findings led to a suggestion for further research in possible implications of sexual size dimorphism on adaptability of incubation at different temperatures. The decrease in incubation shown at dusk may have been due to Black Skimmers taking advantage of a period requiring less nest temperature regulation to forage.

It can be concluded that Black Skimmers are specialised to the dynamic and extreme environment they nest in, but whether they and other floodplain avifauna will adapt to the potential impacts of anthropogenic changes occurring in Amazonia remains to be investigated.

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Appendix 1

In this appendix rankings of incubation behaviour GLMMs within Δ10AIC$_c$ of the lowest raking model are presented for both the second and third attempt (A2 & A3). Parameter estimates of the most parsimonious model with AIC$_c$ value ≤ Δ2 of the lowest ranking model are presented in section 3.5; Table 10. The following are the cosinor set of functions as indicated with i, ii and iii:

i) I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24))

ii) I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24))+I(cos(2*2*pi*Hour/24))+
I(sin(2*2*pi*Hour/24))

iii) I(cos(2*pi*Hour/24))+I(sin(2*pi*Hour/24))+I(cos(2*2*pi*Hour/24))+
I(sin(2*2*pi*Hour/24))+ I(cos(3*2*pi*Hour/24))+I(sin(3*2*pi*Hour/24)).

Appendix 1: Table 1: AIC$_c$ ranking of GLMMS within Δ10AIC$_c$ of the lowest raking model. Response variable is incubation probability for A2.

Model Variables	K	AIC$_c$	ΔAIC$_c$	AIC$_c$Wt
Incubation ~ iii + Days Until Hatching + Ambient Temperature + (1|Nest ID)	10	12872.06	0.00	0.65
Incubation ~ iii + Days Until Hatching + (1|Nest ID)	**9**	**12873.51**	**1.45**	**0.31**
Incubation ~ iii + Days after Julian Date + (1|Nest ID)	9	12879.14	7.08	0.02
Incubation ~ iii + Days after Julian Date + Ambient Temperature + (1|Nest ID)	10	12879.37	7.31	0.02

Appendix 1: Table 2: AIC$_c$ ranking of GLMMS within Δ10AIC$_c$ of the lowest raking model. Response variable is incubation probability for A3.

Model Variables	K	AIC$_c$	ΔAIC$_c$	AIC$_c$Wt
Incubation ~ iii + Days Until Hatching + Ambient Temperature + (1|Beach ID/Nest ID)	**11**	**14102.01**	**0.00**	**0.83**
Incubation ~ iii + Days Until Hatching + (1|Beach ID/Nest ID)	10	14105.14	3.13	0.17

Appendix 1: Table 3: AIC$_c$ ranking of GLMMS within Δ10AIC$_c$ of the lowest raking model. Response variable is sleeping posture probability for A2.

Model Variables	K	AIC$_c$	ΔAIC$_c$	AIC$_c$Wt
Sleeping Posture ~ iii + Days Until Hatching + Ambient Temperature + (1|Nest ID)	**10**	**49805.12**	**0.64**	**0.64**
Sleeping Posture ~ iii + Days after Julian Date + Ambient Temperature + (1|Nest ID)	10	49806.26	1.15	0.36
Sleeping Posture ~ iii + Ambient Temperature + (1|Nest ID)	9	49814.63	9.51	0.01

Appendix 1: Table 4: AIC$_c$ ranking of GLMMS within Δ10AIC$_c$ of the lowest raking model. Response variable is sleeping posture probability for A3.

Model Variables	**K**	**AIC$_c$**	**ΔAIC$_c$**	**AIC$_c$Wt**
Sleeping Posture~ iii + Days Until Hatching + Ambient Temperature + (1|Beach ID/Nest ID)	**11**	**38943.63**	**0.00**	**0.92**
Sleeping posture~ iii + Ambient Temperature + (1|Beach ID/Nest ID)	10	38948.45	4.82	0.08

Appendix 1: Table 5: AIC$_c$ ranking of GLMMS within Δ10AIC$_c$ of the lowest raking model. Response variable is proportion male incubation for A2.

Model Variables	**K**	**AIC$_c$**	**ΔAIC$_c$**	**AIC$_c$Wt**
Prop. Male Inc. ~ iii + Days Until Hatching + (1|Nest ID)	**9**	**1008.67**	**0.00**	**0.62**
Prop. Male Inc. ~ iii + Days Until Hatching + Ambient Temperature + (1|Nest ID)	10	1010.46	1.79	0.25
Prop. Male Inc. ~ ii + Days Until Hatching + (1|Nest ID)	7	1014.03	5.36	0.04
Prop. Male Inc. ~ iii + (1|Nest ID)	8	1015.15	6.48	0.02
Prop. Male Inc. ~ ii + Days Until Hatching + Ambient Temperature + (1|Nest ID)	8	1015.40	6.73	0.02
Prop. Male Inc. ~ iii + Days After Julian Day + (1|Nest ID)	9	1016.55	7.88	0.01
Prop. Male Inc. ~ iii + Ambient Temperature + (1|Nest ID)	9	1016.95	8.23	0.01
Prop. Male Inc. ~ iii + Days After Julian Day + Ambient Temperature + (1|Nest ID)	10	1018.61	9.93	0.00

Appendix 1: Table 6: AIC$_c$ ranking of GLMMS within Δ10AIC$_c$ of the lowest raking model. Response variable is proportion male incubation for A3.

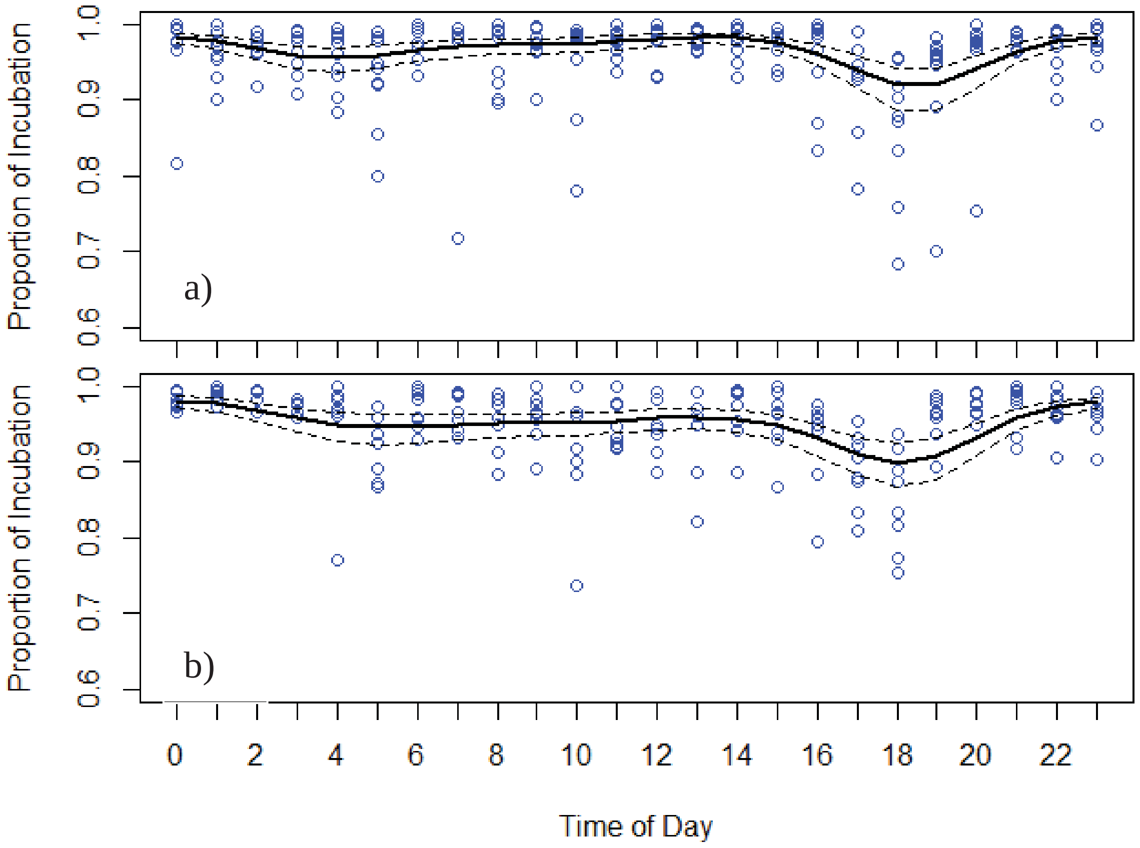
Model Variables	**K**	**AIC$_c$**	**ΔAIC$_c$**	**AIC$_c$Wt**
Prop. Male Inc. ~ Days Until Hatching + (1|Beach ID/Nest ID)	**4**	**799.93**	**0.00**	**0.31**
Prop. Male Inc. ~ Days Until Hatching + Ambient Temperature + (1|Beach ID/|Nest ID)	5	800.35	1.41	0.26
Prop. Male Inc. ~ iii+ Days Until Hatching + (1|Beach ID/|Nest ID)	10	801.38	1.45	0.15
Prop. Male Inc. ~ iii+ Days Until Hatching + Ambient Temperature + (1|Beach ID/|Nest ID)	11	802.02	2.08	0.11
Prop. Male Inc. ~ i + Days Until Hatching + Ambient Temperature + (1|Beach ID/|Nest ID)	7	802.81	2.88	0.07
Prop. Male Inc. ~ i + Days Until Hatching + (1|Beach ID/|Nest ID)	6	803.23	3.29	0.06
Prop. Male Inc. ~ ii + Days Until Hatching + (1|Beach ID/|Nest ID)	8	806.21	6.27	0.01
Prop. Male Inc. ~ ii + Days Until Hatching + Ambient Temperature + (1|BeachID/Nest ID)	9	806.59	6.66	0.01

Appendix 1: Table 7: AIC_c ranking of GLMMS within $\Delta10\text{AIC}_c$ of the lowest raking model. Response variable is incubation bout length for A2.

Model Variables	**K**	**AIC_c**	**ΔAIC_c**	**AIC_cWt**
Incubation Bout Length ~ iii + log10(Ambient Temperature) + Male or Female + (1|Nest ID)	11	13412.96	0.00	1

Models for A3 with incubation bout length are not presented due to overdispersion and lack of fit.

Appendix 2



Appendix 2: Figure 1: Blue circles represent mean proportion incubation per hour per nest from the actual data. Prediction (solid line) and 95 % CI (dashed lines) for incubation probability across time of day in a) A2 and b) A3. These were calculated from the respective best ranked GLMMs presented in Table 10. The comparison shows the good fit of predictions to the actual data despite slight overdispersion of models. Note that the scale on the y-axis is between 0.6 and 1.0.

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