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Distribution, Abundance and Habitat Selection by Breeding Yellow-billed Terns (*Sternula superciliaris*), Large-billed Terns (*Phaetusa simplex*) and Black Skimmers (*Rynchops niger)* in the Brazilian Amazon

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Abstract.—The distribution and abundance of Yellow-billed Terns (*Sternula superciliaris)*, Large-billed Terns (*Phaetusa simplex*) and Black Skimmers (*Rynchops niger*) were estimated, and the effects of habitat features on site occupancy by colonies of these three species nesting in the Anavilhanas Archipelago, Amazonas, Brazil, were examined. Individuals were recorded on beaches during the 2008 and 2009 breeding seasons, with 26 (2008) and 30 (2009) potential nesting beaches (sites) surveyed. In both years, one site included 28% of all the Yellow-billed Terns, while two sites included 65% of all the Large-billed Terns. Site occupancy, the probability that a site is occupied (range ψ), was moderate to low for all three species, but higher for Yellow-billed Terns (0.58-0.63) than for Large-billed Terns (0.40-0.50) and Black Skimmers (0.23-0.54). Yellow-billed and Large-billed terns and Black Skimmers generally nested on larger beaches on islands that had little vegetative cover and that were exposed to open water, remote from river margins, distant from other islands and closer to large colonies of the same species. Abundance estimates (individuals per breeding season in the archipelago ± SE) in 2009 varied considerably among species (Yellow-billed Terns: 192 individuals ± 1; Large-billed Terns: 80 ± 1; Black Skimmer: 31 ± 1). These results suggest that habitat features that influence breeding site use by Yellow-billed and Large-billed terns and Black Skimmers include physical and vegetation characteristics as well as social attraction. While the probability of site occupancy increased with measures related to beach size and geographical isolation, closeness to large colonies indicates the relevance of social interactions for these species and, as such, the importance of large areas for the occurrence of their colonies. *Received 24 November 2010, accepted 1 September 2013.*

Key words.—Amazon, Anavilhanas National Park, Black Skimmer, breeding, freshwater archipelago, Large-billed Tern, *Phaetusa simplex*, *Rynchops niger*, site occupancy, *Sternula superciliaris*, Yellow-billed Tern.

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Little is known about the autecology, ethology and breeding biology of floodplain birds in the Amazon region of Brazil (Petermann 1997) in spite of the vast extent of aquatic environments in the Amazon (Scott and Carbonell 1986). Water level is probably the main factor influencing the timing of the breeding season for ground-nesting floodplain birds (e.g., Bolster and Robinson 1990), because it regulates the availability of sandbanks and beaches along river margins (Preston 1962; Alsdorf *et al.* 2000). However, in tropical wetlands the spatial and temporal interactions between floodplain birds and their habitats are poorly understood, especially within the large Amazon Basin (Petermann 1997).

The recognition of associations between environmental features and species occurrence and abundance can be useful in understanding the factors determining metapopulation dynamics (MacKenzie and Kendall 2002; Kissling *et al.* 2007). It is important to consider both the physical and biotic factors that influence the distribution and abundance of a species' population to make robust estimates of population size and trends (Kissling *et al.* 2007). Estimating changes in population size is a fundamental issue in making sound conservation decisions (MacKenzie and Kendall 2002; Duca *et al.* 2009).

Some of the factors known to influence species distribution and abundance are resource availability, environmental conditions and intra- and interspecific interactions (Begon *et al.* 2006). Use of a site for nesting can be influenced by environmental features at different spatial scales (Boe 1993). The distribution of floodplain birds nesting on beaches within the Amazon Basin is probably influenced by site availability at the regional level. For example, within an archipelago, beaches, and therefore also nesting birds, can be restricted to the main river channel. At the local level, resource availability, such as an area of unoccupied bare sand, might influence the use of a site for nesting. Determining which factors influence the occurrence and abundance of colonial waterbirds may increase our understanding of the mechanisms involved in colony formation. For colonial birds, nesting in groups can be advantageous, for example by reducing predation risk (Erwin 1977), although it may increase competition for food and space to nest (Moller 1987). Hence, the presence and abundance of other individuals of the same or other species may influence breeding site use (Custer *et al.* 1980).

The Anavilhanas Archipelago in the Central Amazon is a freshwater archipelago of about 300 islands with gradients in habitat characteristics that provide opportunities to test hypotheses related to bird responses to habitat features. The archipelago is also part of the Anavilhanas National Park (NP), and the results of this work will be included in the Park's management plan. A more comprehensive approach to address species' responses to environmental variation requires evaluation of environmental variables at a broader spatial scale than usually obtained from field measurements (Kerr and Ostrovsky 2003).

The influence of habitat type and availability on the abundance and occurrence of other species of terns (*Sterna* spp.) and Black Skimmers (*Rynchops niger*) has been investigated previously, mainly in coastal or saline habitats (e.g., Gochfeld 1983; Erwin and Smith 1985; Simmons *et al.* 1998; Scarton 2008). Only a few studies have been conducted in freshwater or interior habitats (e.g., Kirsch 1996; Raeder 2003).

Black Skimmers nest mostly on beaches on the southeastern coastline of North America (Portnoy *et al.* 1981; Krannitz 1989; but see Molina 1996). In South America, Black Skimmers usually nest with Yellow-billed (*Sternula superciliaris)* and Large-billed (*Phaetusa simplex*) terns on sandy beaches and sandbars of rivers and lakes of the Amazon and Paraná River systems (Preston 1962; Groom 1992; Raeder and Bernhard 2003; Maugeri 2005). Nests of Yellow-billed Terns, Large-billed Terns and Black Skimmers (hereafter "terns and Black Skimmers") are formed of simple, shallow scrapes in the sand with neighboring nests often only being separated by a few meters or less (R. Zarza, unpubl. data). In the Amazon and Pantanal floodplains, beaches and sandbars become available for a few months when water levels drop (Raeder and Bernhard 2003), offering an ideal opportunity to evaluate the spatial distribution of tern and Black Skimmer breeding sites (Krannitz 1989).

The results presented here are the first to document tern and Black Skimmer breeding colony distribution and the influence of site features on the occupancy probabilities of nesting adults in Central Amazonia. These are also the first estimates of the occupancy of Yellow-billed Terns and Large-billed Terns using detection probabilities.

The objectives of the study were to: 1) describe the distribution of tern and Black Skimmer breeding colonies in the Anavilhanas Archipelago; 2) estimate the probability of site occupancy by the three species across the archipelago during the 2008 and 2009 breeding seasons and the influences of habitat features on such probabilities; and 3) develop an unbiased estimate of the populations of the three breeding species in 2009.

METHODS

Study Area

Surveys were conducted on islands of the Anavilhanas Archipelago, Amazonas, Brazil (02° 03' S and 03° 02' S, 60° 22' W and 61° 12' W). The archipelago forms part of the Anavilhanas NP, which is managed by Instituto Chico Mendes, Brazil, and is located in the eastern portion of the Amazonas state. Anavilhanas NP covers an area of 350,000 ha, including the entire archipelago of the Negro River and an extensive area covered with terra firme, a forest not inundated by flooded rivers, on the left (eastern) margins of the river (Fig. 1). The ar-

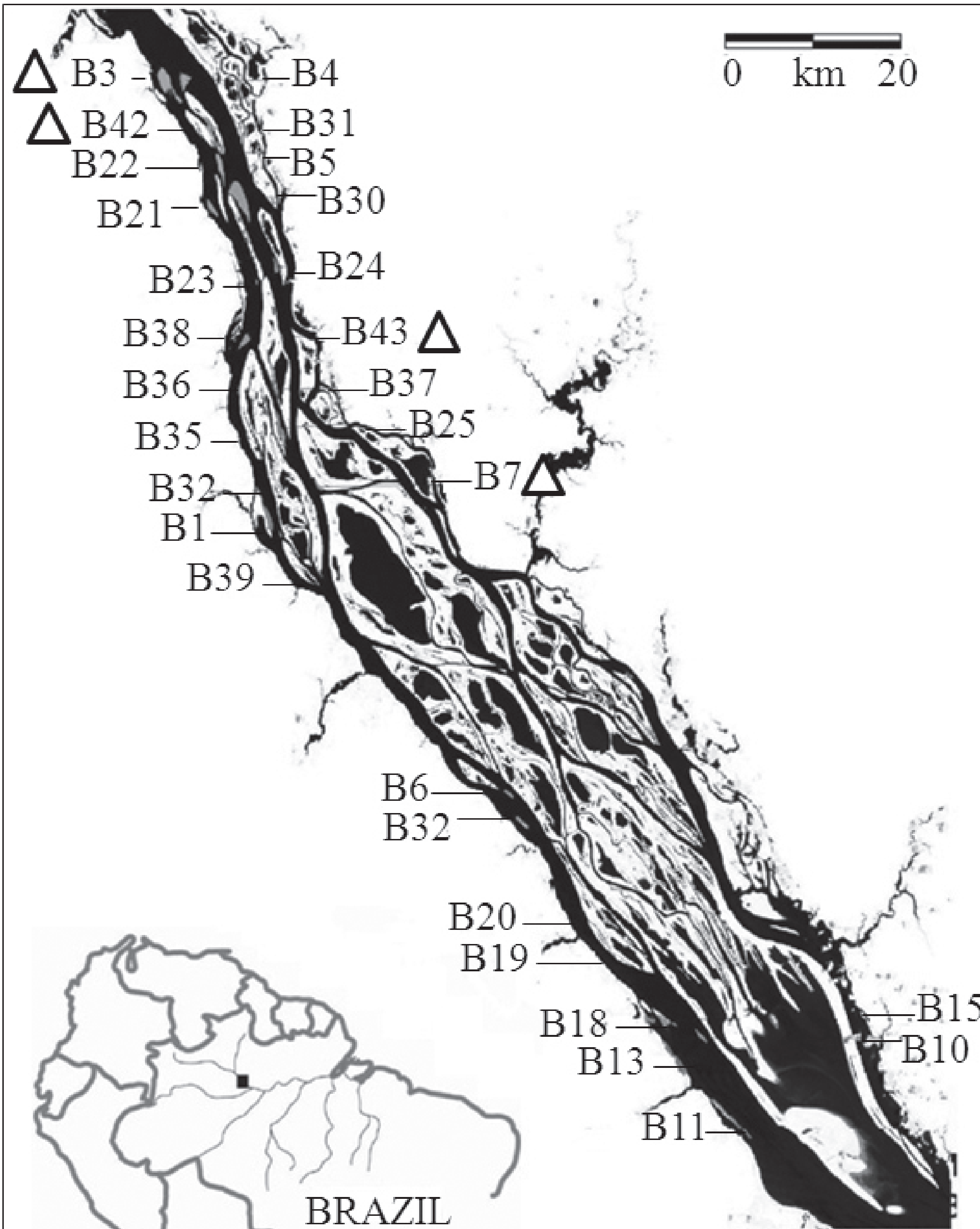

Figure 1. Location of the Anavilhanas Archipelago and identity of the surveyed beaches (B1-B43). Beaches surveyed only in 2009 are marked with a triangle (△).

chipelago is mainly covered by 100,000 ha of Igapó, a seasonally flooded forest inundated by black water but relatively poor in nutrients (Prance 1980).

The main Negro River reaches up to 20 km in width; however, the river channel in the area where the sand beaches were located ranges from 1-3 km. River depth varies seasonally by up to 10 m (UNESCO 2008). During the dry season (September to December), water levels drop and expose sandbanks and beaches on the islands, providing breeding habitat for terns and Black Skimmers. More information describing the environments of the Anavilhanas Archipelago is available in Cintra *et al.* (2007) and Cintra (2012).

Field Methods

Beach availability in the Anavilhanas Archipelago depends on the river level during the dry season and varies among years. Field surveys occurred from 23 October to 1 December 2008 and from 29 October to 21 December 2009, covering most of the dry season in the study area when terns and Black Skimmers were nesting. To locate the potential nesting sites available each year, the Negro River was navigated from the northern to southern boundaries of the Anavilhanas Archipelago (a distance of approximately 150 km). The geographic coordinates of each sand beach on the islands and all the available sandbars were recorded using a GPS. All beaches available during each year were included in the surveys.

Each available beach was visited two to five times, and the presence/absence, as well as the number (count data), of breeding terns and/or Black Skimmers detected were recorded each time using an adaptation of the point count approach (Hutto *et al.* 1986). The results of the repeat surveys (2008: n = 26 beaches; 2009: n = 30 beaches) were used to create the detection histories for each surveyed beach. All presence/absence data were collected by the same observer and in similar weather conditions. Because all available beaches were included in surveys, sampling points (beaches) were not at fixed distances to each other. Nevertheless, we are confident in the independence of the recorded data, considering that it is unlikely that the same individuals would nest on multiple beaches within the relatively short duration of the surveys. Nests of terns and Black Skimmers were searched at each beach to confirm the use of the site for breeding. At the commencement of the surveys, nests already had eggs and no chicks were found. Most chicks hatched after about the same period, at approximately 8 days after the surveys began. We addressed the breeding status, as well as nesting activity and reproductive success for another study, and we are confident that most of the individuals recorded during the present study were engaged in breeding activities.

Statistical Analysis

The probabilities of occupancy and detection were estimated for the Anavilhanas Archipelago as a whole and for each beach based on the detection (presence/absence) histories of all the surveys using the maximum-likelihood inference, implemented in the program PRESENCE (MacKenzie *et al.* 2002; Hines 2006). To test for the influences of physical characteristics and vegetative cover on the probability of site occupancy, we used a hierarchical multi model comparison approach, also based on the maximum-likelihood inference and implemented in PRESENCE (MacKenzie *et al.* 2002; Hines 2006). The model comparison is explained in more detail below.

Seven explanatory variables were chosen to compare occupancy models (Table 1). These variables were not significantly inter-correlated and were selected among a larger set of variables of habitat features related to the physical configuration, vegetation characteristics and social attraction to which birds would be exposed on surveyed beaches. The seven variables used in model building included beach area, beach proximity, island proximity, distance to river margin, beach exposure to open water, distance to the main (larger) colony in the region and island vegetative cover. Because the three species are simple to identify, beach area was the only explanatory variable considered in detection estimates. Descriptions of these variables are provided in Table 1.

Beach areas, island areas and percentage of vegetative cover of the islands were measured in Global Mapper (Blue Marble Geographics 2009) and a color composition of a Landsat TM-5 rectified image. Beach exposure was measured by superimposing a circle shapefile over a Landsat TM-5 rectified image (Instituto Nacional de Pesquisas Espaciais 2008). The circle covered the largest beach surveyed and the surrounding water. The circle was centered on each beach and the proportion of the circle area not occupied by land was calculated in ArcView (Environmental Systems Research Institute 2000). Direction and fetch from wind were not considered in estimating the exposure. The medium proximity index (MPI; de Oliveira and Vettorazzi 2002) was used to measure beach proximity. MPI considers an average distance and area of sites according to a predefined ratio with respect to the site of interest. Because of the spatial configuration of the Anavilhanas Archipelago, rather than a predefined ratio, the distance of the nearest five beaches to each beach was used for the beach MPI, and the distance of the nearest five islands to each beach was used as the island MPI. The distance from each beach to the nearest point on both river margins was used as the distance

Table 1. Description and codes for the seven explanatory variables considered in the model comparison.

Variable Name	Code	Description
Island vegetative cover	VG	Proportion of vegetative cover of the island area
Beach area	S	Beach area (km^2)
Beach proximity index	BP	Measure of site isolation with respect to other beaches
Island proximity index	IP	Measure of beach isolation with respect to islands
Distance to river margin	RM	Distance (km) from the beach to the nearest point on both river margins
Exposure	EXP	Exposure of the beach to open water
Distance to main colonies	COL	Distance (km) to the colony with the highest number of adults in the region for each species

to river margin. The Nearest Features extension (Jenness 2007) implemented in ArcView (Environmental Systems Research Institute 2000) was used for distance measurements.

The Akaike Information Criterion (AIC) or its variants were used to select models from the presence/absence data, and also from the count data. The AIC is an information-theoretic measure that explains variation in the data and the number of parameters (Burnham and Anderson 2002). Because AIC values are on a relative scale, it is recommended that the differences between AIC values (ΔAIC) over all the candidate models in the set are used (Burnham and Anderson 2002). The model with the lowest AIC value (i.e., ΔAIC = 0) was considered to provide the best fit to the data. However, detection and occupancy models with ΔAIC ≤ 2 were also considered for inferences, as these were not significantly different from the model with the lowest AIC value (Burnham and Anderson 2002).

To test the model fit to data for occupancy estimates, 100 parametric bootstraps were run with the program PRESENCE, using the procedure described by MacKenzie and Bailey (2004). Overdispersion of the data was indicated by the value of the variance inflation factor – $\hat{c}$ superior to 1. As suggested by MacKenzie and Bailey (2004), a quasi-likelihood (Q) AIC criterion was used in the model selection for overdispersed data and standard errors were inflated by the value of $\sqrt{\hat{c}}$. AIC criteria were used for model selection from non-overdispersed detection/non-detection data. AIC and QAIC were computed using the program PRESENCE. The strength of the association between each explanatory variable and site occupancy in best fit models was evaluated by the untransformed parameter (beta) estimated in the model. Because occupancy models use logistic regressions, PRESENCE includes a logit link that transforms probabilities in odds ratios and compares the natural log of odds to the explanatory variables, thus rendering linear regressions, with the slope (beta) values indicating the strength of the association between site occupancy and each variable (MacKenzie *et al.* 2002; Hines 2006).

Abundance of breeding adults was estimated for each species using two different approaches. During the 2008 breeding season, one primary observer counted the maximum number of tern and Black Skimmer individuals in each colony among surveys. During the 2009 breeding season, the double-observer approach (Nichols *et al.* 2000a) was used to estimate detection probabilities, which were used to provide unbiased estimates of abundances of the nesting birds. For the double-observer approach, two observers visited each colony together and, in silence, counted the number of birds seen. Species and observer identity were the two variables included in the models for estimating detection probabilities. Because birds flushed as the observers approached the beaches, observers recorded only one point count for each beach. Detection probabilities and abundances were therefore estimated for the Anavilhanas Archipelago as a whole with the double-observer approach.

The statistical population of inference considered in the study was the number of individuals estimated to occupy the surveyed beaches within the archipelago. However, it is difficult to determine the precise geographical limits of the studied populations or what fractions of the populations were estimated in the study. In spite of the increased difficulty and expenses associated with estimating abundance (number of individuals) as compared to occupancy (proportion of area occupied), studies of colonial birds based solely on occupancy estimates offer little information about the size of populations, information that is crucial to monitoring and conservation plans. Occupancy estimates, on the other hand, offer a practical guide to locate specific species needs in terms of area or habitat requirements, and represent an index of relative abundance that may also be used for monitoring species trends. However, such an index would be bound in comparison to abundance estimates, because it is based solely on presence/absence data and, as such, its application should be considered with caution. Nevertheless, there is an expected association between both indexes, because abundance affects the probability of occupancy.

The modelling procedure used in the double-observer approach is detailed in Nichols *et al.* (2000a) and described briefly here: x_{ij} was the number of birds counted by observer i (i = 1, 2) on each beach when observer j (j = 1, 2) was the primary observer, p_i was the detection probability for observer i, and p was the probability of a bird being detected by at least one observer [$p = 1\text{-}(1\text{-}p_1)\ (1\text{-}p_2)$]. Bird detection probabilities were then estimated as $p_1 = (x_{11}x_{22} - x_{12}x_{21})(x_{11}x_{22}+x_{22}x_{21})^{-1}$, $p_2 = (x_{11}x_{22}-x_{12}x_{21})(x_{11}x_{22}+x_{22}x_{12})^{-1}$, and $N = (\sum x_{ij})p^{-1}$. The program DOBSERV (Nichols *et al.* 2000b) was used to obtain estimates for detection probabilities by observers, as well as species occupancy and abundance estimates for each species.

For model selection using detection probability estimates from the count data, a second-order AIC (AICc), with a small sample size bias adjustment, was used as recommended by Burnham and Anderson (2002) when n is small in relation to the number of parameters. AICc was computed using the program DOBSERV (Nichols *et al.* 2000b).

RESULTS

In 2008, all 26 beaches available within the archipelago were surveyed. During the 2008 breeding season, nesting Yellow-billed Terns were detected at 15 beaches, Large-billed Terns at 13 beaches, and Black Skimmers at 14 beaches, while 10 beaches were unoccupied. In 2009, four additional beaches were available and included in the surveys (Fig. 1). Nesting Yellow-billed Terns were detected at 19 beaches in 2009, including two new sites not available in 2008;

whereas Large-billed Terns were detected at 12 beaches, one of which was a new site, unavailable in 2008, and Black Skimmers were detected at seven beaches, all of which were also occupied in 2008. A total of 13 beaches were reused for nesting in 2009 by Yellow-billed Terns (87% of sites used in 2008) and 10 by Large-billed Terns (77% of sites used in 2008). Seven beaches were not used by terns or Black Skimmers in either 2008 or 2009. Beaches used in either breeding season ranged from 1-230 km^2, whereas beaches not used ranged from 9-42 km^2.

Evidence of overdispersion of the presence/absence data for Yellow-billed Terns (2008: $\hat{c}$ = 1.72, P = 0.12; 2009: $\hat{c}$ = 3.13, P = 0.03) and Large-billed Terns in 2009 ($\hat{c}$ = 2.18, P = 0.05) was provided by a goodness-of-fit simulation. Data for Large-billed Terns in 2008 ($\hat{c}$ = 0.87, P = 0.29) and for Black Skimmers (2008: $\hat{c}$ = 0.73, P = 0.49; 2009: $\hat{c}$ = 0.16, P = 0.87) did not present any evidence of overdispersion. The overall site occupancy (ψ ± SE) was intermediate and varied little among species and years, with the exception of estimates for Black Skimmers (Yellow-billed Terns = 0.58 ± 0.10 and 0.63 ± 0.09; Large-billed Terns = 0.50 ± 0.10 and 0.40 ± 0.09; Black Skimmers = 0.54 ± 0.09 and 0.23 ± 0.07, in 2008 and 2009, respectively). The overall detection probability, p ± SE, was high for the three species in both years (Yellow-billed Terns = 0.83 ± 0.05 and 0.87 ± 0.03; Large-billed Terns = 0.87 ± 0.05 and 0.73 ± 0.06; Black Skimmers = 0.83 ± 0.06 and 0.94 ± 0.04, in 2008 and 2009, respectively).

The best supported occupancy and detection probability models in each breeding season revealed some differences between species, particularly in the first breeding season, in which occupancy probabilities responded to a different set of explanatory variables among species. While Yellow-billed Terns were affected only by distance to the main colony and beach area, occupancy by Large-billed Terns and Black Skimmers was affected by beach area, river margin and island proximity. Black Skimmers were also affected by beach proximity. In 2009, the three species were affected by all seven variables. The estimated parameters for models with ΔQAIC or ΔAIC ≤ 2 for the three species in the 2008 and 2009 breeding seasons are summarized in Table 2.

The observed direction and magnitude of the effects of the explanatory variables on occupancy probabilities also varied among species. Because all variables affected the occupancy probabilities of all species in 2009, and because the effects of the variables that affected occupancy probabilities in both years were similar within a species, only results for 2009 with the strongest effects are illustrated for each species (Fig. 2). The occupancy probabilities of the terns and Black Skimmers were positively influenced by increasing beach area and negatively influenced by beach and island proximity in both breeding seasons, with the exception of beach proximity for Yellow-billed Terns in 2008. In 2008, proximity to river margins also affected negatively the probability of being occupied by Large-billed Terns and Black Skimmers, whereas occupancy by Yellow-billed Terns decreased with increasing distance to main colonies. In 2009, the probability of occupancy was also positively related to distance to river margin and beach exposure, and negatively related to the percentage of island vegetative cover and the distance to main colonies. Yellow-billed Terns also presented a positive relationship with beach proximity and island proximity in this season.

A total of 133 Yellow-billed Terns, 72 Large-billed Terns and 103 Black Skimmers were estimated during the 2008 breeding season. Total estimates for the 2009 breeding season were 195 Yellow-billed Terns, 79 Large-billed Terns and 31 Black Skimmers. Comparing the two breeding seasons, the numbers of birds estimated at each nesting site varied the most between sites for Yellow-billed Terns and Black Skimmers, whereas Large-billed Terns were the most consistent.

One site, B10, hosted the main colony of Yellow-billed Terns in the archipelago, about 28% of the total number of birds counted for this species, in both years. The other sites had heterogeneous colony sizes, ranging from two to 20 Yellow-billed Terns. Two sites, B30 and B38, hosted the main colonies of

Table 2. Site occupancy and detection probability models for Yellow-billed Tern (YBTE), Large-billed Tern (LBTE) and Black Skimmer (BLSK), for the 2008 and 2009 breeding seasons in the Anavilhanas Archipelago. QAIC < 2.0 are presented. Abbreviations in model names: S, Beach area; RM, Distance to river margin; EXP, Exposure; VG, Island vegetative cover; BP, Beach proximity index; IS, Island proximity index; and COL, Distance to main colonies.

Species/Year	Model	ΔQAIC	QAIC Weight	Model Likelihood	Number of Parameters
YBTE/2008	ψ(COL),p(.)	0	0.28	1.00	3
	ψ(S+COL),p(.)	0.52	0.21	0.77	4
YBTE/2009	ψ(.),p(.)	0	0.16	1.00	2
	ψ(IS),p(.)	1.30	0.08	0.52	3
	ψ(S),p(.)	1.53	0.07	0.47	3
	ψ(RM),p(.)	1.55	0.07	0.46	3
	ψ(VG),p(.)	1.68	0.07	0.43	3
	ψ(EXP),p(.)	1.78	0.07	0.41	3
	ψ(.),p(S)	1.84	0.06	0.40	3
	ψ(COL),p(.)	1.91	0.06	0.39	3
	ψ(BP),p(.)	1.96	0.06	0.38	3
LBTE/2008	ψ(S+RM+IS),p(.)	0	0.46	1.00	5
LBTE/2009	ψ(.),p(.)	0	0.10	1.00	2
	ψ(.),p(S)	0.73	0.07	0.70	3
	ψ(S),p(.)	0.82	0.07	0.66	3
	ψ(BP),p(.)	0.83	0.07	0.66	3
	ψ(EXP),p(.)	1.37	0.05	0.50	3
	ψ(COL),p(.)	1.64	0.05	0.46	4
	ψ(RM),p(.)	1.69	0.05	0.46	4
	ψ(VG),p(.)	1.79	0.05	0.44	3
	ψ(IS),p(.)	1.87	0.05	0.43	3
BLSK/2008	ψ(S+RM+IS),p(.)	0	0.30	1.00	5
	ψ(S+RM+BP),p(.)	1.14	0.17	0.57	5
	ψ(S+RM),p(.)	1.69	0.13	0.43	4
BLSK/2009	ψ(VG+EXP),p(.)	0	0.14	1.00	4
	ψ(VG+EXP+BP),p(.)	1.30	0.14	1.00	5
	ψ(VG+EXP+S),p(.)	1.39	0.08	0.60	3
	ψ(VG+EXP+RM),p(.)	1.75	0.07	0.52	5
	ψ(VG+EXP+COL),p(.)	1.94	0.18	0.50	5
	ψ(VG+EXP+IS),p(.)	1.97	0.06	0.45	3

Black Skimmers in 2008 and the main colonies of Large-billed Terns in 2008 and 2009. The number of Large-billed Terns estimated at sites B30 and B38 represented about 65% of the total population; the counts ranged from two to four individuals at the other sites. The number of breeding Black Skimmers estimated at sites B30 and B38 represented 75% of the total number of birds of this species estimated in 2008; two to five individuals were counted at every other site. Colony sizes of Black Skimmers were more homogeneous in 2009, ranging from two to eight adults per site.

The best supported model for the count data in 2009 included species and observer identity as explanatory variables for estimates of detection probability. The model including the observer identity was also supported by ΔAIC_c of 1.74 and by a non-significant difference from the best supported model. The probability that a bird would be detected when two observers were estimating bird numbers was 0.99 for the three species and varied little between observers (Yellow-billed Terns: 0.96 ± 0.04 vs. 0.85 ± 0.03; Black Skimmers: 0.96 ± 0.04 vs. 0.80 ± 0.07; and Large-billed

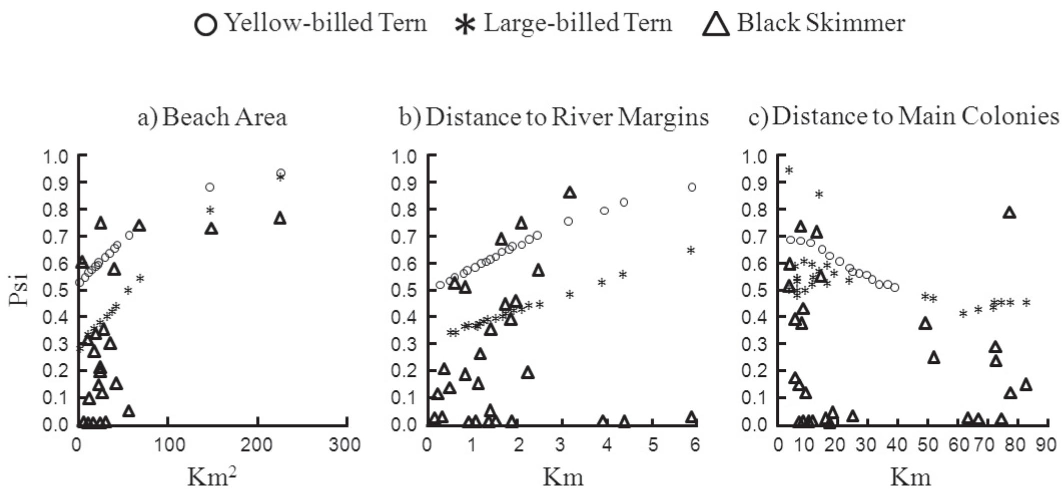

Figure 2. Relationship between site occupancy probabilities (Psi) and a) beach area, b) distance to river margin and c) distance to main colony for Yellow-billed Terns (circles), Large-billed Terns (stars) and Black Skimmers (triangles) in the 2009 breeding season.

Terns: 0.94 ± 0.03 vs. 0.91 ± 0.03). Abundance estimates (n ± SE) for 2009 were 192.36 ± 1.24 for Yellow-billed Terns, 79.56 ± 0.77 for Large-billed Terns and 31.22 ± 0.48 for Black Skimmers.

Discussion

Terns and Black Skimmers were not present on all available beaches during the surveys. Yellow-billed Terns were present at more sites than Large-billed Terns and Black Skimmers in both years, and, in 2009, Black Skimmers were present on only half of the beaches where the species was detected in the previous year. The high proportion of nesting sites reused by Large-billed Terns, the colonization of only two new sites despite more being available, and the similarity in numbers of pairs using the same sites both years suggest colony site tenacity for this species. Yellow-billed Terns seemed to have lower colony site tenacity and more plasticity in using new sites, compared to Large-billed Terns. Although Yellow-billed Terns reused a high proportion of the nesting sites, they selected six new sites when more sites were available and the numbers of pairs using each site varied between years. The decrease in the proportion of sites occupied by Black Skimmers, despite high site reuse, suggests a decline in the numbers of breeding adults in 2009, possibly due to variation in availability of proper nesting habitat for the species.

No previous records of the distribution of breeding colonies and colony site use by terns and Black Skimmers in the study area were available for comparison with our results. In the Solimões River, and also within the Amazon Basin, nesting site tenacity over 3 years has been reported for one Large-billed Tern colony by Raeder (2003), but Gochfeld and Burger (1996) indicate an unpredictability in colony locations as a result of changes in use of nesting sites among years for tern species. Gochfeld (1978) suggested that colonies of Black Skimmers on river beaches and sandbars should show less site fidelity, as found here, because these sites are ephemeral within and among years.

The estimates of the proportion of area occupied by terns and Black Skimmers in the present study were similar to the results reported by Groom (1992). Groom (1992) found that 45% of beaches were used by these three species at the Manú River in the Peruvian Amazon. Non-detection of the three species from a considerable proportion of available beaches suggests differentiation in habitat use, and the model selection suggested that nesting site occupancy may be influenced by a combination of features related to habitat and social attraction in these birds. While the probability of site occupancy increased with measures related to beach size and geographical isolation, closeness to large colonies indicates the relevance of social interactions for these species and, as such, the importance of large areas for the occurrence of their colonies. Variation in landscape features caused by natural fluctuations in the water level, such as the distances between islands, beach exposure and vegetative cover, could affect both food availability and protection against predators and might, therefore, explain variation in habitat use between breeding seasons. For instance, in 2009 there was a large dry-out of the Amazonian rivers, including the Negro River, which created a substantial increase in beach areas within the archipelago. This new landscape scenario certainly increased the availability of beaches and, therefore, their use for nesting by the birds.

During the present study, nesting terns and Black Skimmers preferred to use larger beaches and islands with little vegetative cover in the Anavilhanas Archipelago. Larger islands usually present a greater extent of vegetative cover, where more diverse environments can be found and, therefore, are more suitable to support the habitats needs of most birds (Hildén 1965). However, in some areas, larger islands may also create risks, because vegetation may offer habitat for predators (Burger 1981; Erwin *et al.* 1995), in spite of also serving as cover from heat and a place to hide from predators, as observed for terns (Burger and Gochfeld 1988). Finally, vegetation succession on older islands can lead to desertion of the sites by nesting terns and also influence site fidelity because of a reduced area being available, as shown in the northern hemisphere (Soots and Parnell 1975; Burger 1982).

Terns and Black Skimmers also preferred more isolated sites that were more distant from river margins and/or other islands and presented higher exposure to open water. Terns and Black Skimmers are mainly piscivores (Willard 1985), and the observed higher occupancy probabilities for beaches that are more exposed to open water may be related to increased opportunities for terns and Black Skimmers to forage closer to their nest sites in these habitats. Geographical isolation of preferred beaches may further suggest a role for avoidance of higher predation risk from nearby margins and other islands. Further studies focusing on the foraging and predation ecology of the terns and Black Skimmers from the Anavilhanas Archipelago may contribute to the understanding of the factors leading to the patterns of habitat utilization observed here.

In the present study, social attraction appeared to play an important role in colony site choice for Large-billed Terns and Black Skimmers, as these two species were concentrated in two main colonies with only one or two pairs nesting at other sites. The sites closer to the main colonies also showed a higher probability of being occupied. Conspecific attraction seemed to be more important for Yellow-billed Terns, as most of their colonies were larger monospecific colonies. The smaller influence that distances to any beach had on site occupancy for Yellow-billed Terns in 2009 may be a result of their wider distribution that year. In colonial birds, the abundance of other individuals is a major attractant in colony establishment; only the first pair chooses a breeding site based on non-social cues (Heinänen *et al.* 2008). Thus, interspecific or intraspecific attraction is essential for breeding site selection in colonial species (Heinänen *et al.* 2008). If there is sufficient resource availability, little disturbance and high previous breeding success, more individuals tend to colonize the site and the probability of birds attaching to existing colonies are high (Matthiopoulos *et al.* 2005).

Excluding the main colonies, the number of individuals of the three species in most colonies in Anavilhanas was similar to the one to 12 pairs per colony reported by Groom (1992) for the Manú River, Peru. The numbers of Large-billed Terns and Black Skimmers in Anavilhanas reported here were lower compared to colony sizes registered by Krannitz (1989) for one colony at the Trombetas River (approximately 242 pairs of Large-billed Terns and approximately 74 pairs of Black Skimmers), and much smaller than the estimates made by Raeder (2003) at one sandbank in the Solimões River (9,822 pairs of Large-billed Terns and 1,743 pairs of Black Skimmers). The difference in abundance between the results of the present study and those reported for the Solimões River colony could be explained by the higher productivity and increased food resources in whitewater rivers such as the Solimões River, compared with blackwater rivers such as the Negro River. Production of phytoplankton is thus higher in white water floodplains, although the periphyton is reduced along mainstreams (Puttz and Junk 1997) and fish abundance is lower due to overfishing (Batista and Pretere 2007). Raeder (2003), however, attributes this great concentration of Large-billed Terns and Black Skimmers in a single Solimões River colony to there being no other suitable nesting sites available, with other potential sites being disturbed by either cattle ranching or egg harvesting. Because the Anavilhanas Archipelago is part of a national park, no cattle ranching or human settlements are permitted in the complex; thus, tern and Black Skimmer colony distributions should reflect responses to a relatively natural set of biological and physical factors.

The accuracy of estimates of regional population size for most waterbird species are questionable and rarely is there any formal assessment of accuracy for count estimates (Morrison *et al.* 2006). The Neotropical Waterbirds Census is the main source of data for estimates of waterbird population sizes in the Neotropics (Espinosa 2008); however, methods to account for detection probability estimates are not considered in these counts, nor are detection probabilities considered in abundance estimates (see López-Lanús and Blanco 2005). Information about population sizes has an intrinsic biological importance (Morrison *et al.* 2006). Accurate measurements of waterbird population sizes in particular have become considerably important in conservation planning; for example, they are used to assess the importance of sites for protection under the Ramsar Convention on Wetlands of International Importance and as Important Bird Areas (Delany *et al.* 2006; Morrison *et al.* 2006).

Documenting colony site fidelity and identifying major colony sites are important for the Anavilhanas Archipelago park management plan. Long-term colony monitoring needs to be maintained to assess colony site fidelity both in the region and elsewhere in Brazil and South America.

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