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Breeding dynamics and population trend in the largest colony of the Red-footed Booby *Sula sula* (Linnaeus, 1766) in the South Atlantic

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Keywords: Breeding seasonality; Fernando de Noronha archipelago; seabirds; tropical region.

ABSTRACT – Understanding breeding parameters based on standardized surveys represents a great indicator for evaluating long-term changes and population trends, especially in seasonal species. Here, we performed monthly monitoring of large and independent colonies of the Red-footed Booby *Sula sula* in the Fernando de Noronha archipelago during 2018–2024, focusing on recognize the breeding dynamic and population trends. We found well synchronized colonies, following clear seasonal patterns in six defined breeding seasons (during c. 15 months). Breeding adults were recorded throughout the year, with peaks of active nests in August (34.75 ± 8.80 nests/ha) and total abundance in June (50.84 ± 11.46 individuals/ha). Active nests and breeding adults remained stable over the study period. The abundance of adults in the colonies was increased, in response to increases in non-nesting individuals, which points to population recruitment. This is corroborated by the increase in breeding success across the seasons, which varied considerably (c. 8-40%). Our data provided the first continuous census over the years for the Red-footed Booby. We highlight that continued long-term monitoring is crucial for understanding the population dynamics of the largest colonies of this seabird in the South Atlantic region.

Dinâmica reprodutiva e tendência populacional na maior colônia do atobá-de-pé-vermelho *Sula sula* (Linnaeus, 1766) no Atlântico Sul

Palavras-chave: Reprodução sazonal; arquipélago de Fernando de Noronha; aves marinhas; região tropical.

RESUMO – Entender os parâmetros reprodutivos com base em levantamentos padronizados é um ótimo indicador para avaliar mudanças de longo prazo e para avaliar tendências populacionais, especialmente em espécies sazonais. Neste estudo, monitoramos mensalmente três colônias amplas e independentes do atobá-de-pé-vermelho *Sula sula* (Linnaeus, 1766) durante 2018–2024 no arquipélago de Fernando de Noronha, com foco em reconhecer a dinâmica reprodutiva e as tendências populacionais. Foram observadas colônias sincronizadas, seguindo claros padrões sazonais, durante seis temporadas reprodutivas bem definidas (com duração média de 15 meses). Adultos reprodutivos foram registrados ao longo de todo ano, com picos de ninhos ativos nos meses de agosto (34,75 ± 8,80 ninhos/ha) e abundância total de indivíduos em junho (50,84 ± 11,46 indivíduos/ha). O número de ninhos ativos e de adultos reprodutivos permaneceu estável ao longo do período de estudo. A abundância de adultos nas colônias foi crescente, em resposta ao aumento de indivíduos não-nidificantes, apontando para um recrutamento populacional. Isso é corroborado pelo aumento do sucesso reprodutivo ao longo das temporadas reprodutivas, a qual variou consideravelmente (c. 8-40%). Nossos dados forneceram o primeiro censo contínuo ao longo dos anos para o atobá-de-pé-vermelho. Reforçamos que a continuidade dos monitoramentos a longo prazo se torna fundamental para entender a dinâmica populacional das maiores colônias desta ave marinha na região do Atlântico Sul.

Dinámica reproductiva y tendencia poblacional en la mayor colonia del piquero Patirrojo *Sula sula* (Linnaeus, 1766) en el Atlántico Sur

Palabras clave: Reproducción estacional; archipíelago de Fernando de Noronha; aves marinas; región tropical.

RESUMEN – La comprensión de los parámetros reproductivos basados en estudios estandarizados es un excelente indicador para evaluar los cambios a largo plazo y para evaluar las tendencias poblacionales, especialmente en especies estacionales. En este estudio, monitoreamos mensualmente grandes colonias independientes del Piquero Patirrojo *Sula sula* (Linnaeus, 1766) durante 2018–2024 en el archipiélago de Fernando de Noronha, con un enfoque en el reconocimiento de la dinámica reproductiva y las tendencias poblacionales. Se observaron colonias sincronizadas, siguiendo patrones estacionales claros, durante seis temporadas reproductivas bien definidas (con una duración media de 15 meses). Se registraron adultos reproductivos en todos los meses del año, con picos de nidos activos en agosto (34,75 ± 8,80 nidos/ha) y abundancia total de individuos en junio (50,84 ± 11,46 individuos/ha). El número de nidos activos y de adultos reproductivos se mantuvo estable a lo largo del periodo de estudio. La abundancia de adultos en las colonias aumentó en respuesta al incremento de individuos no nidificantes, lo que apunta a un reclutamiento de la población. Esto lo corrobora el aumento del éxito reproductivo a lo largo de las estaciones reproductivas, el cual varió notablemente (c. 8-40%). Nuestros datos proporcionaron el primer censo continuo a lo largo de los años para el Piquero Patirrojo. Destacamos que un monitoreo continuado a largo plazo es crucial para comprender la dinámica poblacional de las mayores colonias de esta ave marina en la región del Atlántico Sur.

Introduction

Understanding breeding activity in seabirds is one of the most effective ways to understand population sizes and their oscillations[1][2][3]. The resilience and size of colonies over time can reflect the quality and resources of their breeding sites, since seabirds connect terrestrial and marine environments and processes[4][5]. Thus, standard censuses focusing on seabird activity are relevant to take effective actions for conservation purposes[6][7], especially when considering protected nature areas (e.g., Marine Protected Areas – MPAs) that often provide a refuge for numerous individuals[8]. Seabirds are known to be one of the most globally threatened groups[7], making it necessary to better understand how populations are reacting across time and under local conditions in different regions, especially considering breeding dynamics[9][10][11]. In this context, Brazilian tropical waters comprise a large territory in the South Atlantic Ocean, with c.100 seabird species, which have been little studied by long-term surveys focusing on comprehensive demographic and phenology traits[12][13].

One of the most iconic seabird that is threatened in Brazil is the Red-footed Booby *Sula sula* (Linnaeus, 1766)[14], the smallest booby species among the Sulidae (60 cm; 1 kg), which presents two distinguished morphs – brown and white individuals[15][16]. This is an arboreal seabird species and some breeding features are known, such as formed nests with a single clutch size and nest-guarding by pairs during c. 45 days of hatching and c. 120 days of fledging time[17][18][19][20]. The foraging habits of this species are pelagic by fishing in flight or diving very effectively[17] and differ according to time of day[21]. The species is non-migrant in widespread tropical global areas, restricted to offshore regions[16][22]. In the Atlantic, Red-footed Booby populations occur largely in the Caribbean region and in a few oceanic islands in the South[16]. Among them, there are low numbers of breeding pairs on Ascension Island and Saint Helena[23][24][25][26], while on Trindade Island the species colonies were reported to be extinct, with only a few individuals that are rarely seen[27][28]. The Rocas Atoll and Saint Peter and Saint Paul archipelago receive dispersal individuals in flight and resting[27]. More remarkably, the Fernando de Noronha archipelago still holds colonies that comprise the largest population in the South Atlantic Ocean, with a maximum of 1,440 individuals found in 2011[23][27].

In the current study, we monitored different colonies of the Red-footed Booby population in the Fernando de Noronha archipelago using a standard census. Populational traits were investigated, mainly including the breeding parameters and abundance oscillations over time and sample sites. We analyzed how population size varied across the years, aiming to recognize general trends in the local population, defined seasons, breeding success, and abundance of adults in their colonies. Finally, we also discuss general trends and factors that may affect Red-footed Booby colonies in this tropical oceanic island of the South Atlantic Ocean.

Material and Methods

Study area

The Fernando de Noronha archipelago (hereafter FNA; 03°52′S; 32°25′W) is a volcanic island group situated 345 km off the northeastern mainland with a total land area of 26 km^2 and altitudes up to 323 m [29][30]. The archipelago has a tropical oceanic climate (Awi Koppen classification) with an annual temperature of around 27°C, great interannual variability in the rainfall rate of c. 1,400 mm, and predominant easterly surface winds and South Equatorial currents from the southeast[30][31]. This territory is defined as seasonal deciduous forest, where several environments provide a variety of conditions for local fauna in FNA, especially regarding bird species[32][33][34][35]. The greatest richness of avifauna among the Brazilian oceanic islands is presented in FNA, as the representativeness of an Important Bird Area[34][36]. The region includes about 60 migrant and vagrant species, six landbirds and 11 resident seabirds, highlighting the nationally threatened Audubon's Shearwater *Pufiinus lherminieri* Lesson, 1839, Red-billed Tropicbird *Phaethon aethereus* Brandt, 1840, White-tailed Tropicbird *Phaethon lepturus* Daudin, 1802 and Red-footed Booby *Sula sula* (Linnaeus, 1766)[34][37][14].

The archipelago has two categories of protected areas: the Environmental Protection Area (hereafter APA; 79,136 ha – exclusive region of the Fernando de Noronha; [38]), which comprises a permanent human population of over 3,100 inhabitants who live on the main island[39], and the National Marine Park (hereafter PARNA; 10,932 ha; [40]), under strict protection. Focusing on the long-term monitoring (i.e., [41]) of the Red-footed Booby population, we elected three areas, accessible by trails, as independent sites, containing colonies in isolated environments from each other (Fig. 1): 1) Sancho beach (colony including 5.79 ha): a sandy ground bordered by a steep wooded cliff, which constitutes the first colony of the Red-footed Booby in PARNA, to refer the neighboring area of APA; 2) Golfinhos bay (2.17 ha): a rocky beach associated with coastal arboreal vegetation situated in a no-take zone, and; 3) Buracão cove (5.25 ha): a gentle slope covering a large forest area down to a rocky coastal line. All sites present similar conditions in altitude (c. 0–80 m asl), substrate, and general environment influences, as well as being located in the inland sea waters (North-Northeast direction) of the archipelago within PARNA.

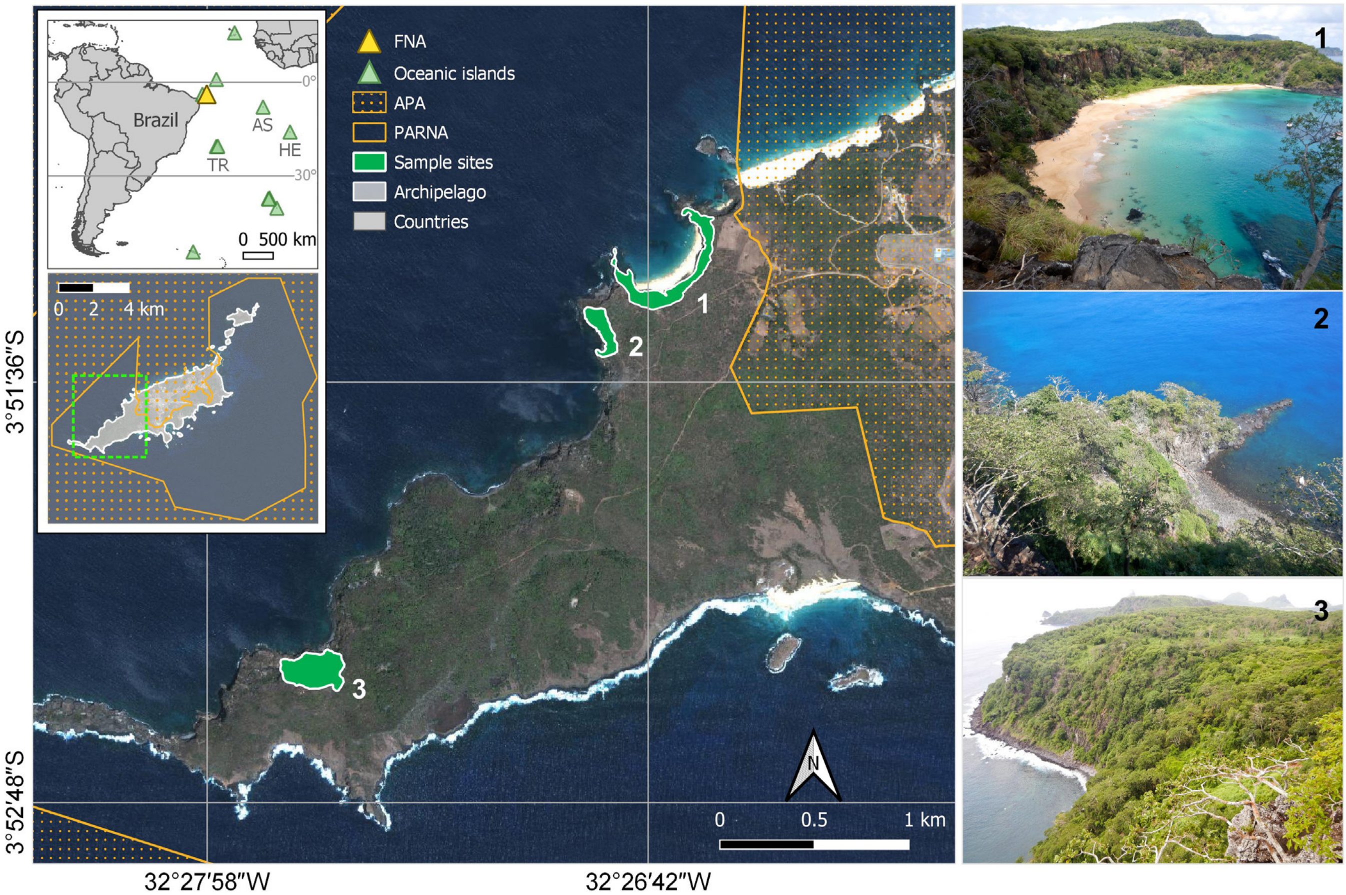

Figure 1 – Map showing the Fernando de Noronha archipelago (FNA) overview with the oceanic island from the Atlantic Ocean (AS = Ascencion, HE = Saint Helena, TR = Trindade), natural protected areas (APA = Environmental Protected Area, and PARNA = National Marine Park) that shelter the archipelago, and the sample sites (1 = Sancho beach, 2 = Golfinhos bay, and 3 = Buracão cove) visited during this study, delimited by three different colonies of the Red-footed Booby *Sula sula* (Linnaeus, 1766).

Data collection

The fieldwork was carried out by the Chico Mendes Institute for Biodiversity Conservation (ICMBio) team (under the permit SISBIO n. 24318), monthly, always in the morning (c. 2 h per site) and accompanied by the same collector (LPSS). The monitoring covered the period from May 2018 to January 2024, except during July 2018 and April, May, and June 2020 (pandemic lockdown). Sancho beach and Golfinhos bay were sampled during the entire period, and sampling in Buracão cove began in November 2020. To survey the Red-footed Booby colonies, we performed distance censuses (binoculus 10 x 42) on foot and from a fixed point, covering the same standardized area at the sampling sites over time. Data were recorded in pencil on a standard field sheet in PVC plate. The main parameter adopted was the number of active nests, corresponding to the monthly sum of 1) incubating adults, and 2) eggs and nestlings with or without adults[42]. The nestlings were identified according to their morphological characteristics[43][44], as follows: A) initial phase: N1 (devoid of feathers), N2 (covered with white feathers), N3 (visible remiges and rectrices feathers), and N4 (completely feathered or with traces of feathers on the head, neck and flanks); and B) final phase: N5 (brown feathered and independent able to fly). Total abundance was defined as the sum of breeding adults (nesting individuals, incubating adults, and adults caring for their nestlings) and non-nesting adults (resting individuals, without nesting activity or parental care, which suggests a non-breeding individual; counted from July 2020) by month.

Data analyses

Breeding seasons (numbered from S18 to S23, in relation to the highest number of months with breeding activity in each year) were defined as the total duration of the first month with breeding adults and the last with the presence of N5, including all sample sites. In cases where the seasons overlap, we defined the lowest number of incubating adults between the seasons as the beginning, as of N5 as the end. The nesting period was defined as the first to the last month in which a nesting adult was detected. The numbers of active nests and abundance per month were taken by summing all sample sites. To interpret the breeding population proportion in each season, we checked the highest percentage of breeding adults and compared this with the total abundance of the same month, comprising the average of all sample sites. We do not discard the possibility that adults could nest more than once per season, so this percentage may refer to the minimum value reached for breeding adults.

To properly compare between sample sites, we took the density values (number of each category per hectare) of active nests, breeding adults, non-nesting adults, and total abundance separately. We evaluated the colonies' synchronicity using Pearson's correlation to compare the density oscillations between the colonies over the entire sample period. Then, we used the Kolmogorov-Smirnov test for normality, Levene's Test for homogeneity of variances, and one-way ANOVA to check the differences in densities between areas, months, years, and seasons. If the sample sites were positively correlated and had homogeneous variances, we would assume that Red-footed Booby population behaves in a similar way, in general, in the FNA. Thus, we used Linear Regression to check populational trends over time, using 1) the general mean density of active nests for causal inference in breeding population, 2) the average abundance densities in general and separately to identify the influence of breeding and non-nesting adults in each colony, and 3) the breeding success parameters. Statistical proceedings were performed in RStudio v.1.2.5042 ($\alpha = 0.05$) and graphs were created in this software and Microsoft 365 Excel ®.

After describing temporal dynamics of breeding and populational trends, we focused on estimate incubation, hatching, and fledging counts in each colony. As our samplings were applied at c. 30 day intervals and without access trees to identify the nest contents, it was not possible to completely define the breeding events and duration of incubation and nestling' phases. According to[18], we assumed hatching (c. 45 days) and fledging (c. 120 days) time to predict the breeding success in each season. In order not to overestimate the number of breeding events per season, we summed interleaved values over two months by referencing the highest values of I) incubating adults (INC), II) N3, to cover all respective hatched initial phase chicks (HAT), and III) N5, to infer fledged chicks (FLE), in each sample site. Thus, we assume that this covered the failed events and reached the minimum of hatched and fledged individuals conservatively. Finally, we defined hatching (HAT/INC x 100), fledging (FLE/HAT x 100) and breeding (FLE/INC x 100) success as percentage for each site, and average between them to infer the entire season (e.g., [45][46]).

Results

We monitored six breeding seasons during 65 sampled months in colonies of the Red-footed Booby in FNA over the study period (Fig. 2). Defined seasonality in breeding activity was observed with great variation in active nests across the months ($F_{11,157} = 21.92$, $p < 0.001$) with the breeding peak occurring in August (34.75 ± 8.80 nests/ha; Fig. 3A). The sample areas were positively correlated and no significant differences in the density of active nests occurred between the colonies (Table 1). The highest number of active nests occurred in the Buracão cove, with 270 nests (51.43 nests/ha) in August 2022 (S22), and the lowest value was found in Golfinhos bay, where no active nests occurred in May 2019 (S19). Breeding seasons were generally characterized by the beginning of nesting adults in January to May and the end in November, regarding an average of nine months with nesting period, and the last breeding adults with nestlings in December. Nestlings represented an average of 38.17 ± 6.76% of the total birds in the colony during the months of breeding peak. Initial phase chicks presented major densities in September (17.87 ± 5.60 nestlings/ha) and final phase chicks in October (8.66 ± 3.65 nestlings/ha), followed by the last fledging nestlings (N5) in March to April. Altogether the breeding seasons totaled an average of 15 months in duration, including four months with the most overlap between them (Table 2).

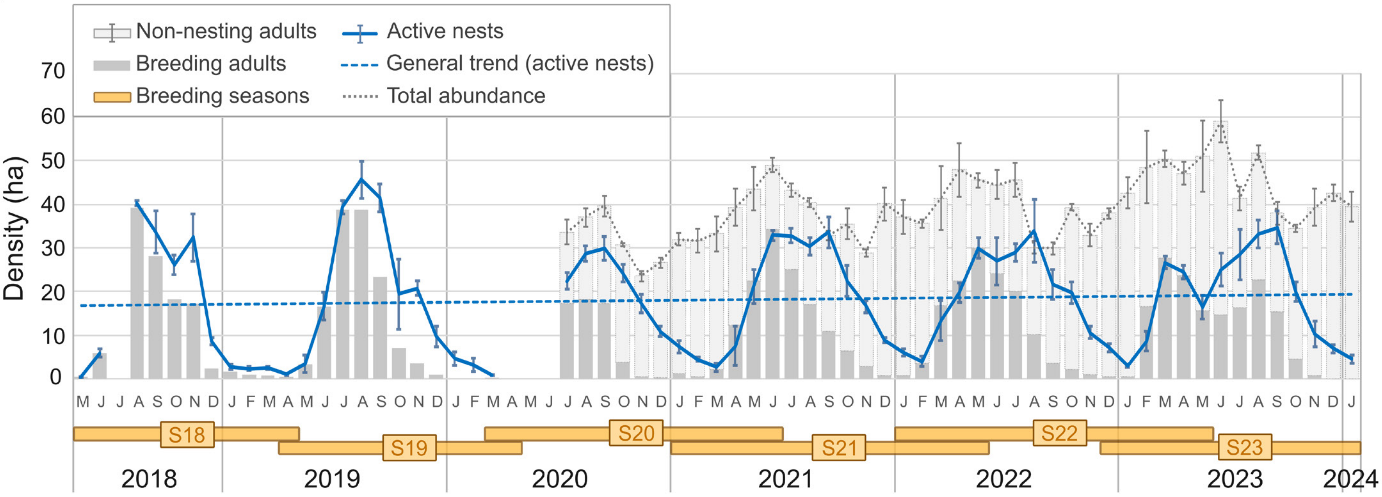

Figure 2 – Temporal trend and categories overview of the Red-footed Booby *Sula sula* (Linnaeus, 1766) colonies in average densities per hectare of active nests (standard bar error in blue), breeding adults, non-nesting adults (standard bar error in gray), and total abundance, including general trend of active nests (blue dashed line) during the study period of May 2018 to January 2024 in the Fernando de Noronha archipelago, Brazil.

Table 1 – Pearson's correlation matrix between sample sites of Red-footed Booby *Sula sula* (Linnaeus, 1766) colonies in relation to the density of active nests, breeding adults, non-nesting adults, and total abundance in the Fernando de Noronha archipelago. Areas below the diagonal of equal values show Pearson's correlation coefficients (r_p) and above the diagonal significant p-values.

Parameters	Sample sites	Sancho	Golfinhos	Buracão
Active nests	**Sancho**	-	<0.001	<0.001
	Golfinhos	0.841	-	<0.001
	Buracão	0.745	0.775	-
Breeding adults	**Sancho**	-	<0.001	<0.001
	Golfinhos	0.831	-	<0.001
	Buracão	0.539	0.764	-
Non-nesting adults	**Sancho**	-	<0.001	0.032
	Golfinhos	0.780	-	0.044
	Buracão	0.343	0.325	-
Total abundance	**Sancho**	-	<0.001	<0.001
	Golfinhos	0.557	-	<0.001
	Buracão	0.578	0.542	-

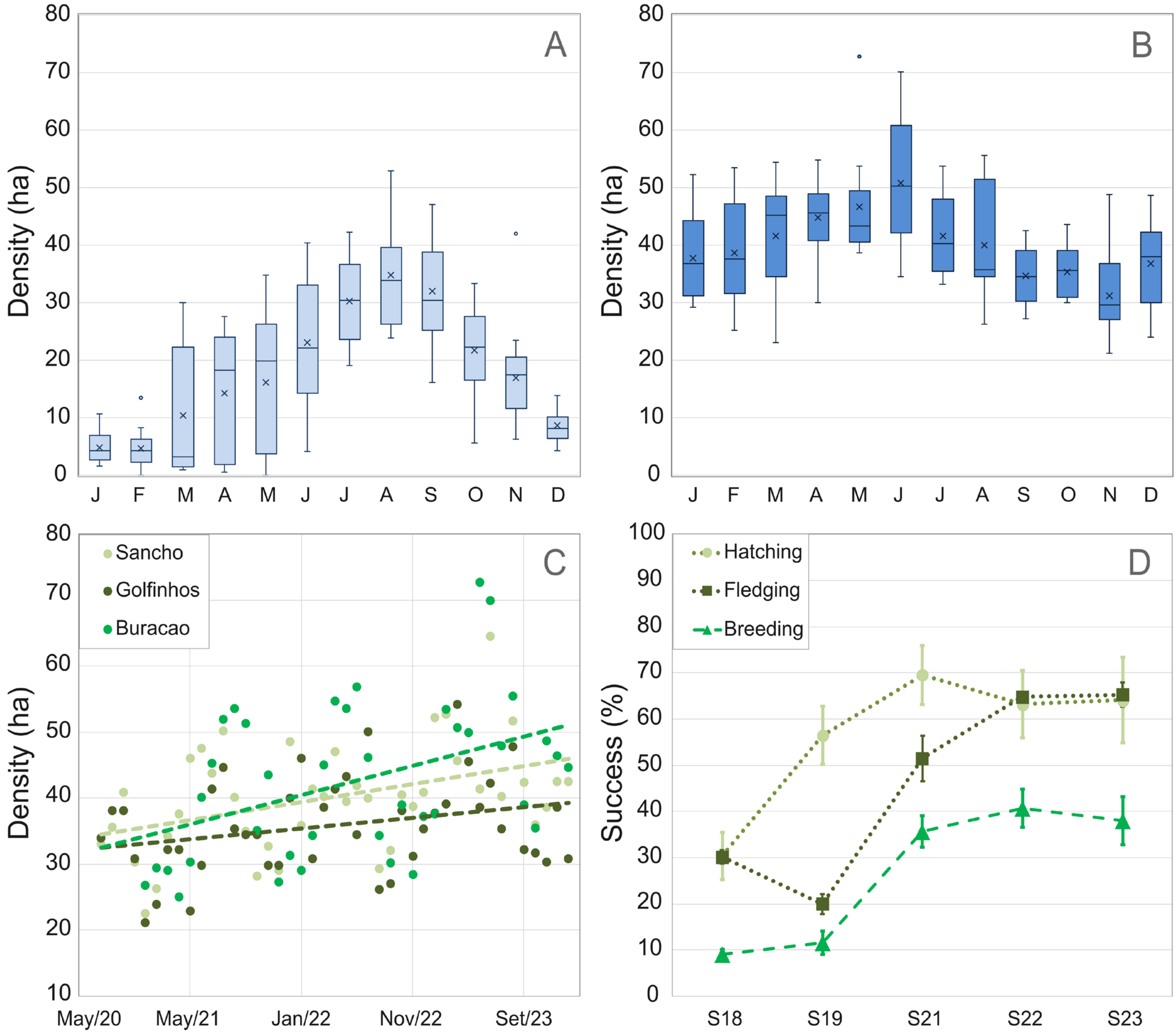

Figure 3 – Red-footed Booby *Sula sula* colonies in the Fernando de Noronha archipelago from May 2018 to January 2024, regarding: A) density of active nests per hectare of all sampled colonies by months; B) density of individuals per hectare of all sampled colonies by months; C) total abundance trends in each sample site over time; and D) percentage of hatching, fledging, and breeding success over the breeding seasons (S18–S23, except of S20).

In general, there is a stable trend comparing the density of active nests over time of the breeding population throughout the sampling period (R^2 = 0.004; p = 0.579), and no significant differences were shown across time ($F_{6,162\ [years]}$ = 0.924; p = 0.479; $F_{5,163\ [seasons]}$ = 0.819; p = 0.538). Despite this, changes were detected throughout the seasons, for example, the delay in the beginning of breeding activities (May to December) and the expansion in total duration time, noting in particular the first seasons (S18–S19) comprising c. 13 months and later seasons (S21–S23) c. 17 months (Table 2).

Table 2 – Breeding and populational parameters of six breeding seasons (S18–S23) of the Red-footed Booby *Sula sula* (Linnaeus, 1766) in the Fernando de Noronha archipelago during the study period from May 2018 to January 2024. Sample sites: SA = Sancho beach; GO = Golfinhos bay; BC = Buracão cove; T = Total values of breeding season overview. * Estimated value.

Season	Sample site	Start (breeding adults)	Peak of active nests	Last incubating adults	Final N5 nestling	Total duration (months)	Average abundance ± SD, (max. in month)	Breeding ind. proportion	Non-nesting ind. proportion	Hatching success	Fledging success	Breeding success
S18	SA	May/18	Aug/18	Mar/19	Apr/19	12	—	—	—	23.01	32.14	7.39
	GO	Jun/18	Sep/18	Jan/19	Apr/19	11	—	—	—	37.50	28.07	10.52
	BC	—	—	—	—	—	—	—	—	—	—	—
	T	**May/18**	**Aug/18**	**Mar/19**	**Apr/19**	**12**	**—**	**—**	**—**	**30.25**	**30.10**	**8.96**
S19	SA	Apr/19	Aug/19	Dec/19	Apr/20*	13	—	—	—	47.54	16.85	8.01
	GO	Jun/19	Aug/19	Dec/19	Apr/20	11	—	—	—	65.41	22.99	15.03
	BC	—	—	—	—	—	—	—	—	—	—	—
	T	**Apr/19**	**Aug/19**	**Dec/19**	**Apr/20***	**13**	**—**	**—**	**—**	**56.48**	**19.92**	**11.52**
S20	SA	Mar/20	Aug/20	Oct/20	Apr/21	14	205 ± 43 (237 Sep/20)	—	—	—	—	—
	GO	—	Sep/20	Oct/20	Apr/21	—	66 ± 12 (83 Sep/20)	66.21	33.79	—	—	—
	BC	—	—	Nov/20	Jun/21	—	—	—	—	—	—	—
	T	**Mar/20**	**Sep/20**	**Nov/20**	**Jun/21**	**16**	**—**	**—**	**—**	**—**	**—**	**—**
S21	SA	Jan/21	Jul/21	Dec/21	Apr/22	16	231 ± 39, (291 Jun/21)	65.98	34.02	65.60	60.68	39.81
	GO	May/21	Sep/21	Jan/22	May/22	13	88 ± 11, (97 Jun/21)	76.28	23.72	84.68	46.81	39.64
	BC	May/21	Sep/21	Nov/21	May/22	13	225 ± 51 (282 Jul/21)	68.13	31.87	58.39	46.96	27.42
	T	**Jan/21**	**Jul/21**	**Jan/22**	**May/22**	**17**	**519 ± 81 (661 Jun/21)**	**70.13**	**29.87**	**69.56**	**51.48**	**35.62**
S22	SA	Jan/22	May/22	Nov/22	Mar/23	15	241 ± 36 (273 Apr/22)	65.06	34.94	48.27	66.88	32.28
	GO	Mar/22	Jul/22	Nov/22	Feb/23	12	80 ± 13 (109 Jul/22)	69.15	30.85	62.10	64.40	40.00
	BC	Feb/22	Aug/22	Dec/22	May/23	16	238 ± 59 (299 Jun/22)	73.24	26.76	79.10	63.02	49.85
	T	**Jan/22**	**Aug/22**	**Dec/22**	**May/23**	**17**	**558 ± 91 (651 Apr/22)**	**69.15**	**30.85**	**63.16**	**64.77**	**40.71**
S23	SA	Dec/22	Aug/23	Nov/23	Apr/24*	17	264 ± 41 (374 Jun/23)	62.74	37.26	69.01	72.96	50.35
	GO	Feb/23	Sep/23	Oct/23	Mar/24*	14	84 ± 15 (118 Mar/23)	56.78	43.22	42.42	80.35	34.09
	BC	Feb/23	Sep/23	Nov/23	Apr/24*	15	269 ± 55 (382 Mar/23)	56.74	43.26	80.80	42.55	34.38
	T	**Dec/22**	**Sep/23**	**Nov/23**	**Apr/24***	**17**	**606 ± 93 (834 Jun/23)**	**58.75**	**41.25**	**64.08**	**65.29**	**39.60**

The colonies were also positively correlated with respect to the density of breeding adults, non-nesting adults, and total abundance (Table 1). Densities of breeding adults did not differ between sample sites ($F_{2,114} = 0.048$; $p = 0.954$) and, although synchronic, significant differences were detected in non-nesting adults ($F_{2,114} = 4.198$; $p = 0.017$) and total abundance ($F_{2,114} = 5.378$; $p = 0.005$), with higher values occurring in Buracão cove (42.70 ± 11.72 individuals/ha). These data were biased by high variations in total abundance in S21 ($F_{2,30} = 4.201$; $p = 0.024$) and S23 ($F_{2,21} = 4.059$; $p = 0.032$). As these were isolated variations, we also assumed similar tendencies in the population of the Red-footed Booby in FNA for these parameters. Significant differences were found in total abundance between months ($F_{11,105} = 4.491$; $p < 0.001$; Fig. 3B), pointing to a seasonal dynamic of adults in their colonies, with highest densities in June (50.84 ± 11.46 individuals/ha) and lowest in November (31.16 ± 7.16 individuals/ha). Covering the period of standardized counting in the three colonies, we observed a general upward trend in the increase in total abundance over time ($R^2 = 0.129$; $p < 0.001$); of note the maximum of 661 individuals in S21 and 834 in S23, reflecting the same pattern in all isolated colonies (Fig. 3C). In fact, the increase in abundance over time was strongly influenced by the non-nesting adults ($R^2 = 0.100$; $p < 0.001$) compared to stable breeding adults ($R^2 = 0.001$; $p = 0.717$). These data suggest a change in population proportion, with the non-nesting adults increasing from 29.87% in S21 to 41.25% in S23, while breeding adults did not differ over time ($F_{4,112\ [years]} = 2.412$; $p = 0.053$; $F_{3,113\ [seasons]} = 0.643$; $p = 0.589$).

Breeding success showed great variation over the seasons, from c. 8% in the first monitored periods to c. 40% in the most recent seasons, which provided for increased parameters in hatching (24%) and fledging (35%) success over time (Fig. 3D; Table 2). Major success occurred in S22 (40.71%) and lower in S18 (8.96%). Sancho beach presented the greatest variations for all parameters, including the highest and lowest values of breeding success (S21: 50.35%; S18: 7.39%, respectively). Despite including few samples, we interpreted that these values for breeding parameters were representative between colonies and reflected similar trends over the seasons, indicating a significant increase in hatching ($R^2 = 0.309$; $p = 0.048$) and fledging ($R^2 = 0.698$; $p < 0.001$). Therefore, the average value for breeding success was 29.53% (IC 95% 18.80–40.26) for the Red-footed Booby colonies in FNA.

Discussion

Seasonality peaks were clear in the breeding seasons of the Red-footed Booby in FNA and there were no differences in temporal trends of the active nests, indicating stability in the breeding population. Our data indicate, in general, synchronized activity in all colonies, with slight changes between sites. Thus, well-defined seasons and similar trends over the years are expected for this population in FNA, although other sites should be further investigated, mainly on adjacent islands. Seasonality breeding patterns were also observed in other regions for this species, such as the Johnston Atoll (North Pacific; [47]) in January to August, and different periods in other localities of the Indian-Pacific Ocean[48][49][50][51]. In addition, a year-round regime with two breeding peaks was characterized with laying varying between different colonies[52][53]. Furthermore, Red-footed Booby colonies also presented non-seasonal breeding activity and some changes in their activity patterns over time may occur, modifying the breeding features across different months[50]. S18 and S19 showed latter and shorter seasons when compared to recent years, suggesting that there may be more stable breeding cycles or intermittent seasons comprising adults in different life cycles. This dynamic is expected for many seabird species, especially for populations with heterogeneous individuals (i.e. regarding different ages of breeding maturity), as already observed for Red-footed Boobies in Pacific Ocean[18][47].

Therefore, total abundance in FNA colonies may also reflect heterogeneous individuals within the FNA population. The continuous increase in non-nesting adults in consecutive years, strongly indicates the recruitment of adults in the first ages within the colonies, although the population structure and adult cycles need to be better investigated. Although some seabirds present low philopatry and many surviving nestlings disperse to other localities (e.g.,[53][54][55]), the Red-footed Boobies in FNA are an isolated population, with few and far suitable environments for dispersion or colonization in the Atlantic, such as Ascension Island (c. 2000 km). This fact is supported by several observations of fledged nestlings (N5), perpetuating throughout the months of the sampling period. In addition, the permanence of adults in the original colonies is associated with good food availability[18]. Ocean barriers restrict gene flow in Red-footed Boobies in this region, showing little evidence of connectivity between the FNA and Caribbean populations[56][57]. Previous studies also pointed to stable trends in the FNA population (see[27]). Nonetheless, [27] occasional observation compilations published with few standardizations between them, could underestimate the number of individuals throughout the whole archipelago (e.g., last surveys in 2011 with 1,440 individuals in May and 733 in July). In the current study, we surveyed the maximum abundance in June 2023, reaching 834 individuals specifically in three isolated colonies (total area c. 14 ha, corresponding to 0.5% of the FNA). Thus, our data indicate that Red-footed Boobies hold a major population in FNA, representing the largest colony in the South Atlantic. The biggest population in the entire Atlantic remains in the Caribbean region, with around 10,000 breeding pairs[23][58]. It is worth mentioning a declining trend in Red-footed Boobies globally[59].

Breeding success responded rapidly over the seasons, demonstrating that there can be large interannual variations on some occasions. Hatching events were much lower in S18, while fledging events decreased in S19, followed by increasing and similar patterns from S21. This indicates an increase in breeding activity in the population studied during the study period. Previous studies reported higher breeding success (above of 60% , in general) dor other regions, however, previous studies reported higher success (above of 50%, in general) for other regions (e.g.,[60][61][62]), although these colonies were sampled in the past. Long-lived species usually adjust their breeding effort to boost their own survival in response to environmental variability[63][47]. Several studies have found changes in the beginning of breeding in various seabird species, changing to earlier or later breeding or altering the season duration in response to climate oscillations[64]. [65] point out that breeding seasons of the Suliformes are affected by weather and oceanographic conditions, and the period of egg laying can vary in relation to local environment changes. The breeding seasons of the Red-footed Boobies in FNA indicated delay throughout the monitored period, noting that the first breeding adults in S18 started in May and occurred early in S22, starting in January. Although our collected time-series was not so long, we interpret that a longer season is related to the highest breeding success values, as observed in S21–S23, demonstrating the commonest pattern for this species in FNA.

Historically, the FNA population probably declined during the military occupation and penal settlement in the 20th century, when the archipelago endured major deforestation[66]. After that, the colonies seemed to increase locally, and our results corroborate[67] the recent stability, which may be due to implementation of the natural protected areas in the 1980s[38][40]. A well-kept environment could support the local population and restore the correlated resources over the years. Despite this, local pressures can affect the colonies differently. The PARNA shelters all the colonies of Red-footed Boobies and there is no evidence of their occurrence in the associated anthropic zones of APA. Invasive alien species and vegetation composition can be related to seabirds, and may affect the Red-footed Booby population, as a species large-dependent on native plant species[68][26][16]. For instance, one of the most visited places in FNA is Sancho beach, with around 164,000 visitors in 2022 alone[69]. Although no significant differences were observed between the sampling areas, we noted higher averages of active nests in Buracão cove (20.55 ± 14.41 nests/ha), where a continuous colony is located, with consistent native vegetation. These data should be further investigated in consecutive years, to predict how local pressures can affect colony sizes and breeding traits. The most stringent precautions need to be taken in visitation, management, and biosecurity procedures, since population declines can result from rapid environment changes (e.g.,[70][62][71]).

Tropical seabirds typically have longer breeding seasons and their activities are closely tied to environmental conditions[72][73][74][75][76]. The significant oscillation of adults between months suggests a pattern of individuals returning to their colonies, with individuals leaving after the period of nestling dependence. This is probably the most regulatory moment for the seasonality mechanism and breeding performance of Red-footed Boobies, possibly connected with optimal conditions of climate oscillations, such as water productivity and, consequently, food availability. Although FNA waters are considered as oligotrophic, seamount formation in this region generates the formation of upwelling processes and nutrient accumulation[77][78]. [79] reported that the highly pelagic Masked-Booby *Sula dactylatra* Lesson, 1831 tends to remain closer, also as a resident population to the FNA, besides suggesting that similar abundances in flying fish should be presented throughout the year. Thus, by observing segregate trophic position[80], it could be expected that species display different breeding strategies in the same site.

Conclusion

The time-series presented by the monitoring in the current work enable greater understanding about the largest colony of Red-footed Boobies in the entire South Atlantic region, providing a relevant baseline to regard the demographic traits of this species over time. We were able to observe strong breeding seasonality of the species in FNA, presenting different dynamics over time, such as: 1) stable breeding population through active nests and breeding adults; 2) increase in total abundance; and 3) fast interannual variations for breeding success. Following the suggestion of[27], we provide a continuous census over several years and reinforce that long-term surveys are recommended to properly monitor this population. Isolated study areas, such as the mid-Atlantic refuge in FNA, can provide great information to better understand global changes and compare several populations.

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