UPWELLING LINKS REPRODUCTIVE SUCCESS AND PHENOLOGY IN TROPICAL BROWN BOOBIES *SULA LEUCOGASTER*

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ABSTRACT

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For organisms living in seasonal environments, timing of breeding is key to ensuring reproductive success. Accordingly, temperate and polar seabird species follow seasonal pulses, matching their breeding events with peaks in ocean productivity. However, the seasonality of breeding has been much less explored in tropical seabirds. Here, we report seasonal variation in oceanography that affects reproductive success of the Brown Booby *Sula leucogaster*, a species widely distributed in the tropics. We monitored 61 nests during the 2019 breeding season at Bona Island, Gulf of Panama, and collected remote-sensing information for upwelling, sea-surface temperature, rainfall, chlorophyll-α concentration, wind speed, and wind direction. We used egg/chick survival probability and a sliding-window statistical approach to assess temporal changes in reproductive success. Maximum chlorophyll-α concentrations (linear and quadratic expressions) had the strongest influence over survival probability in the two to three weeks prior to the death of the egg/chick. After model averaging, we found that survival probability was positively correlated with maximum chlorophyll-α (confidence interval CI(β) = 0.19 to 2.54 mg/m^3) and negatively correlated with (maximum chlorophyll-α)^2 (CI(β) = −4.19 to −0.31 mg/m^3). In addition, survival probability decreased with later laying dates (CI(β) = 0.43 to 1.74 days), indicating that chicks born earlier in the breeding season had higher chances of survival. Given the correlation between chlorophyll-α and upwelling, we concluded that Brown Booby reproductive success in the Gulf of Panama is influenced by upwelling and that breeding in this tropical species follows seasonal pulses like those observed in polar and temperate species.

Key words: Brown Booby, chlorophyll-α, survival probability, timing of reproduction, seasonal pulses

INTRODUCTION

Seabirds often live in seasonal environments where the timing of breeding (i.e., laying date, chick rearing) is key to ensuring reproductive success (Perrins 1970, Verhulst & Nilsson 2008). Many seabirds follow seasonal pulses, matching their breeding events with peaks in ocean productivity when food is abundant enough to maintain themselves and their chicks (Perrins 1970). Strong seasonality has been widely documented in seabirds breeding at high latitudes, where laying date, clutch size, and fledgling production are often strongly linked to food availability (Shultz *et al.* 2009, Hatch 2013, Gaston & Elliott 2014). Although tropical seabirds usually have longer breeding seasons, their timing of breeding and degree of reproductive success may be constrained by environmental conditions and food availability. For example, some tropical species like the Peruvian Booby *Sula variegata* and the Peruvian Pelican *Pelecanus thagus* adjust their timing so they can raise their chicks when food availability is higher (Passuni *et al.* 2016). Other booby species fail at (Nazca Booby *S. granti*; Champagnon *et al.* 2018) or skip (Red-footed Booby *S. sula*; Cubaynes *et al.* 2011) reproduction during unfavorable conditions like El Niño events.

The Pacific coast of Central America is a highly dynamic environment (O'Dea *et al.* 2012), where strong winds from the Caribbean drive seasonal upwelling in certain regions along the Pacific coast (Xie *et al.* 2005). In the Gulf of Panama, upwelling occurs during January to May (dry season). This causes its usually warm surface waters (sea-surface temperature (SST) > 27 °C; annual range 18.0–27.7 °C) to cool, promoting enrichment of nutrients (nitrate, phosphate, orthosilicic acid) in the euphotic zone. Part of this response is a peak in surface chlorophyll-α concentration (1.5 mg/m^3, annual range 0.24–1.44 mg/m^3; D'Croz & O'Dea 2007). These changes in temperature, nutrient availability, and phytoplankton concentration promote zooplankton growth (Forsbergh 1969, D'Croz & O'Dea 2007), which is positively correlated with fish abundance (Forsbergh 1969). Thus, such seasonality could potentially affect upper trophic level predators such as seabirds and marine mammals (Thompson *et al.* 2012), including the Brown Booby *S. leucogaster*, a pan- and sub-tropical species (Schreiber & Norton 2020).

The Brown Booby is a long-lived seabird in which members of colonies tend to breed asynchronously, meaning there can be a drawn-out nesting season for a given colony (Nelson 1978). As summarized by Nelson, this booby lays clutches of 1–2 eggs. Pairs share parental care during 42 ± 3 days of incubation and up to five months of brood care, and typically only one offspring survives per reproductive attempt. The species nests along the coast of the Gulf of Panama (Fig. 1), mainly from December to August; a dozen or so breeding pairs are found the rest of the year (HMG pers. obs.). Nesting occurs within a variety of habitats, including flat areas with low-growing shrubs and cacti as well as on rocky cliff faces. This booby feeds mainly on fish along this coast, though specific prey

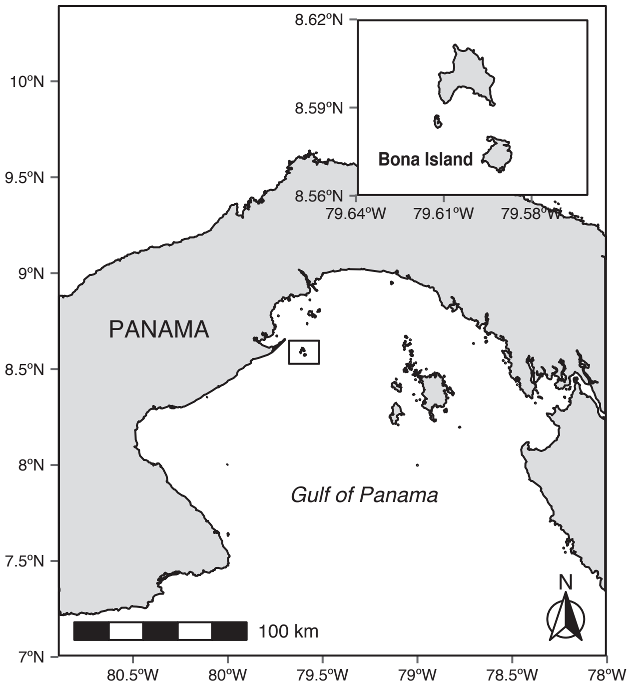

Fig. 1. Location of the Brown Booby *Sula leucogaster* colony at Bona Island, Panama, in the Gulf of Panama.

species are unknown. It appears that Gulf of Panama seabirds breed annually in response to environmental fluctuations associated with seasonal upwelling, which generally occurs from January to May (D'Croz & O'Dea 2007). However, the environmental signals that influence breeding remain unknown.

In this study, we investigated the potential effects of upwelling on the reproductive success of the Brown Booby in the Gulf of Panama. We monitored nests exposed to upwelling and downwelling conditions at Bona Island during the 2019 breeding season to test whether estimated offspring survival probability differed between upwelling or downwelling conditions. We chose to investigate the early life stage (egg/chick), and we predicted that survival probability would decrease as upwelling diminished, due to less favorable environmental conditions.

METHODS

Field work

Bona Island (08°34′25.09″N, 079°35′25.99″W) is a small island of 74.7 ha (0.747 km^2) located 40 km south of Panama City, Panama. Here, we monitored 61 nests (53 unsuccessful and 8 successful) between 02 April and 23 August 2019 (Fig. 1). This island is considered an Important Bird and Biodiversity Area (Angehr 2003, Angehr & Kushlan 2007) and has recently been declared a Wildlife Refuge by the Panamanian authorities (Ministerio de Ambiente 2019). All monitored nests were located in an area measuring 17.85 m^2, which contained ~80% of all breeding Brown Booby pairs in the colony. During this period, members of this colony experienced both upwelling (January to May) and downwelling (June to December) conditions (D'Croz & O'Dea 2007). We registered the GPS location of each monitored nest and recorded the number of eggs, chicks, and fledglings on a weekly basis or when conditions allowed it. To estimate the age of each fledgling, we used a photographic record of each chick at the nest, as well as the minimum laying date or hatching date (~42 days since egg laying; Nelson 1978). We considered a breeding attempt successful if a fledgling (~90 days old) was recorded in the nest.

Remote sensing

We characterized the oceanographic conditions for one year (August 2018 to August 2019) in waters adjacent to Bona Island using remote-sensing information obtained directly from the website of NOAA's Environmental Research Division Data Access Program (Simons 2020). Upwelling was estimated using eight-day averages of Ekman's upwelling measures, which were downloaded from the Metop-B ASCAT satellite with a 0.25° resolution. To determine if other climatic variables had an effect on reproductive success, we estimated daily measures of rainfall (CHIRPS station, 0.05° resolution) and eight-day averages of SST, chlorophyll-α concentration (Aqua MODIS satellite, 0.03° resolution), wind speed, and wind direction (Metop-B satellite, 0.25° resolution) for a grid of 0.5° latitude × 0.5° longitude. This grid size was based on the Brown Booby's maximum foraging distance (50.6 ± 30.5 km; Gilmour *et al.* 2018).

Statistical analysis

We used a sliding-window analysis ("climwin" package for R; van de Pol *et al.* 2016) to identify the climatic predictors that most strongly affected reproductive success. This exploratory approach considered environmental data for a whole year (i.e., the 365 days before the end of the sampling season) to identify the best possible window (see van de Pol *et al.* 2016, MacLeod *et al.* 2018). First, we used egg/chick survival probability as a proxy of reproductive success and built a Cox Proportional Hazard model to assess the time-dependent and time-independent factors that influenced survival probability. We selected a Cox model with laying date as a baseline to account for non-climatic effects on survival probability. We then built candidate models for each climatic variable and compared them against the baseline model to find the best descriptive metric (i.e., minimum, maximum, mean) and the form of the relationship (i.e., linear or quadratic expressions). Based on preliminary tests, we considered sliding windows (i.e., time periods relevant for a biological response) up to 12 weeks prior to the event of interest for all the climatic variables. We identified the best possible relative climatic window (i.e., one window for every individual) for each variable and ran randomized models to assess the likelihood that the best window was a result of over-fitting (van de Pol *et al.* 2016). We found a relevant climatic window for each of the six variables tested.

To confirm the evidence for multiple climatic signals (i.e., critical climatic periods), the best climatic window identified was extracted for every variable. All variables were centered and a correlation matrix was used to detect collinearity among climatic variables. We then built a baseline model including laying date and created 11 hypothesis-based climatic models without highly correlated variables in the same model. Models were ranked using the Akaike Information Criterion, and we selected all models within a cumulative Akaike weight of 0.95 (Burnham & Anderson 2002). All statistical analyses were conducted in R (v.4.0.2; R Development Core Team 2020).

TABLE 1
Models used to explore variation in egg/chick survival probability with oceanographic conditions (n = 61)[a]

Model	Fixed effects[b]	*df*	logLik[c]	AICc	ΔAICc	*wi*
1	*LD + Chl + Chl²*	*3*	*−148.69*	*303.38*	*0.00*	*0.84*
2	*LD + SST + SST²*	*3*	*−150.69*	*307.39*	*4.01*	*0.11*
3	LD + Rain + Rain²	3	−152.13	310.27	6.88	0.03
4	LD + Upwelling + Chl + Chl² + Rain + Rain² + WD	7	−148.20	310.45	7.070	0.02
5	LD + Upwelling	2	−159.91	323.83	20.45	0.00
6	LD + Upwelling + Chl + Rain + WD	5	−157.91	325.85	22.46	0.00
7	LD + WD	2	−163.22	330.44	27.06	0.00
8	LD + WS	2	−164.21	332.42	29.04	0.00
9	LD + Rain	2	−166.44	336.88	33.49	0.00
10	LD	1	−171.13	344.26	40.87	0.00
11	LD + Chl	2	−171.01	346.03	42.65	0.00
12	LD + SST	2	−171.08	346.17	42.78	0.00

[a] AIC: Akaike Information Criterion. Best-fitting models with a cumulative Akaike weight (*wi*) of ~0.95 are in italics.
[b] Chl: Chlorophyll-α concentration, LD: Laying date, Rain: Rainfall, SST: Sea-surface temperature, WD: Wind direction, WS: Wind speed
[c] logLik: Log-likelihood

RESULTS

The best supported models for egg/chick survival probability included laying date as well as maximum chlorophyll-α and minimum SST in its linear and quadratic expressions (Table 1). However, after model averaging, maximum chlorophyll-α (linear and quadratic expressions) was identified as the only climatic predictor for egg/chick survival probability (Table 2; Fig. S1). Based on the sliding-window analysis, maximum chlorophyll-α (linear and quadratic expressions) in the two to three weeks prior to the death of the egg/chick had the strongest influence over survival probability (Fig. 2, S2). Survival probability was positively correlated with maximum chlorophyll-α (confidence interval CI(β) = 0.19 to 2.54 mg/m^3) and negatively correlated with (maximum chlorophyll-α)^2 (CI(β) = −4.19 to −0.31 mg/m^3) (Table 2). The likelihood of a Brown Booby egg/chick dying increased when chlorophyll-α concentrations were between 0 and 0.58 mg/m^3 and decreased at concentrations above 0.58 mg/m^3 (Fig. 3). We did not find direct associations between survival probability and upwelling, SST, rainfall, wind speed, or wind direction. However, as expected, chlorophyll-α (maximum) and SST (mean) were highly correlated (r^2 = −0.67), as were both variables relative to upwelling (r^2 = 0.20, r^2 = −0.33, respectively). In addition, survival probability decreased with later laying date (CI(β) = 0.43 to 1.74 days), indicating that chicks born earlier in the breeding season had higher chances of survival (Fig. 4, Table 2).

TABLE 2
Summary of the averaged model explaining egg/chick survival probability (n = 61)

Predictor[a]	β	Standard error	95% Confidence interval
Laying date	*0.98*	*0.25*	*0.48 to 1.47*
Maximum chlorophyll 2–3 week (mg/m³)	*1.37*	*0.60*	*0.19 to 2.54*
Maximum chlorophyll 2–3 week² (mg/m³)	*−2.25*	*0.99*	*−4.19 to −0.31*
Minimum SST 8th week (°C)	−0.36	0.99	−2.30 to 1.58
Minimum SST² 8th week (°C)	−0.32	0.89	−2.07 to 1.43

[a] SST: Sea-surface temperature. Predictors in italics are the only ones with a statistically significant effect on survival probability.

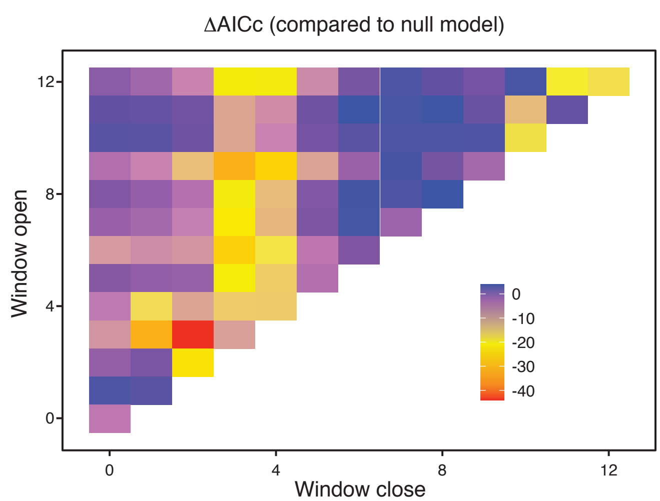

Fig. 2. Heat map of ΔAICc (AICc of null model – AICc of climate model). The best window (in weeks) for chlorophyll-α concentration (quadratic expression) opened 3 weeks and closed 2 weeks before the offspring died. The lowest Akaike Information Criterion values (ΔAICc, red region) indicate the strongest window compared to the baseline model (no climate effects).

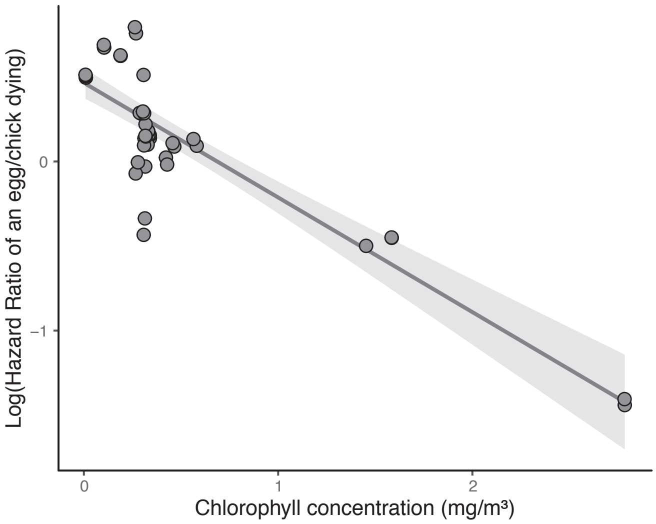

Fig. 3. Hazard ratio of a Brown Booby *Sula leucogaster* egg or chick dying, relative to the maximum chlorophyll-α concentration (linear expression) at sea. The shaded area indicates the 95% confidence interval.

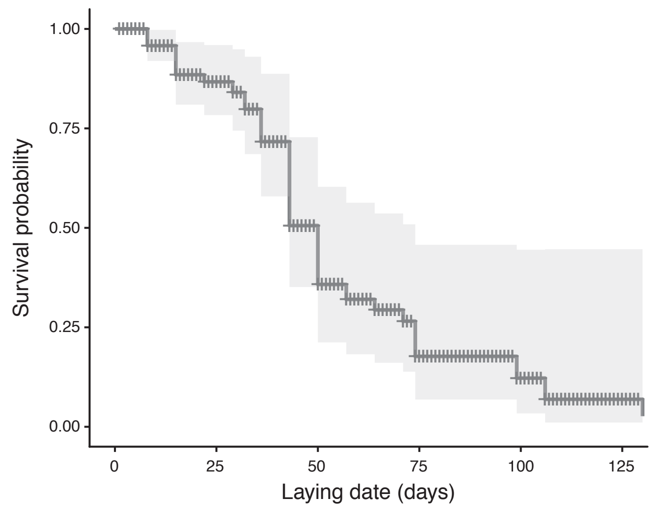

Fig. 4. Brown Booby *Sula leucogaster* egg/chick survival probability in relation to laying date. The shaded area indicates the 95% confidence interval for the survival curve.

Periods of heavy rainfall occurred on 28 May, 23 July, and 30 July, during which the number of active nests at the colony decreased (Fig. 5); as ground-nesting birds, many nests were washed out by the heavy rainfall. Although rainfall was not selected in the best-fitting models (Table 1), steep drops in the number of offspring occurred after each period of heavy rainfall (HMG pers. obs.; Fig. 5). Nest density was higher at the beginning of the season and gradually decreased as the season progressed, but with steep drops after heavy rainfall late in the season.

DISCUSSION

Upwelling conditions throughout our study period positively influenced the reproductive success of Brown Boobies. This is consistent with observations of the species' association with areas of strong upwelling conditions (Heatwole *et al.* 1997), as well as links between foraging strategy and prey availability (Castillo-Guerrero *et al.* 2016). Although Brown Boobies have the capacity to breed almost all year around, those individuals breeding when local chlorophyll-α concentrations were higher had offspring with greater chances of survival. Chlorophyll-α concentration is strongly linked to upwelling conditions when SST is cooler and ocean productivity is higher. This would mean that the Brown Booby is following seasonal pulses, breeding when food availability is likely greater. Similar results have been found in other tropical seabirds. For example, the Guanay Cormorant *Leucocarbo bougainvillii*, Peruvian Booby, and Peruvian Pelican in the northern Humboldt Current System raise their chicks during periods of strong upwelling, when Peruvian anchoveta *Engraulis ringens* are most available (Murphy 1936, Murphy 1981, Tovar *et al.* 1987; Passuni *et al.* 2016). Moreover, our results are consistent with previously observed patterns of high mortality and low reproductive success among seabirds in the Panama Bight, which is associated with abnormally warm SSTs and low primary productivity during strong El Niño events (Murphy 1936, Glynn 1988).

Laying date had a negative effect on chick survival, in accordance with what has been observed as the season progresses among most seabirds species (Perrins 1970). At Bona Island, early breeders had greater reproductive success, probably because they experienced the entire upwelling season, when conditions were more favorable and food was abundant. Reproductive success decreased as the season progressed, probably because late breeders experienced relaxed upwelling or even downwelling conditions, when food was scarce. Our results coincided with a previous study on Brown Pelicans *P. occidentalis* in the Gulf of Panama (Taboga Island), where breeders exposed to early upwelling produced more fledglings and where nest abandonment was correlated to SST (Montgomery & Martínez 1984, Angehr & Kushlan 2007). Age, breeding

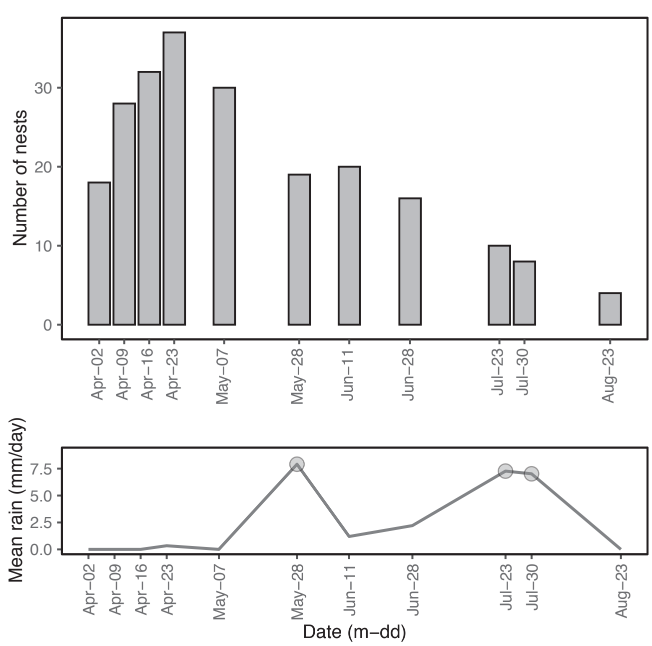

Fig. 5. Number of nests and rainfall (mm) for every day of monitoring at the Brown Booby *Sula leucogaster* colony at Bona Island, Panama. The three rainfall events are marked with a circle.

experience, and body condition are other factors that are known to contribute to the success of early arrivals (Forslund & Pärt 1995, De Forest & Gaston 1996, Whelan *et al.* 2021). In most bird species, including tropical seabird species, early breeders tend to be older and more experienced, which contributes to greater reproductive success (Forslund & Pärt 1995, De Forest & Gaston 1996, McLeay *et al.* 2017). At our study colony, individual age and breeding experience were unknown, so we were unable to consider these factors in our analyses.

In conclusion, Brown Booby reproductive success on the Pacific coast of Panama is highly seasonal and influenced by upwelling conditions, confirming similarity to species in polar and temperate regions. Future research should explore non-climate effects for seabirds in the region and acquire long-term time series data to confirm that the pattern reported in this study is annually consistent.

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