POPULATION ECOLOGY – ORIGINAL RESEARCH

Seasonal weather effects on offspring survival differ between reproductive stages in a long-lived neotropical seabird

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Abstract
Weather conditions can profoundly affect avian reproduction. It is known that weather conditions prior to and after the onset of reproduction can affect the breeding success of birds. However, little is known about how seasonal weather variability can affect birds' breeding performance, particularly for species with a slow pace of life. Long-term studies are key to understanding how weather variability can affect a population's dynamics, especially when extreme weather events are expected to increase with climate change. Using a 32-year population study of the Blue-footed booby (*Sula nebouxii*) in Mexico, we show that seasonal variation in weather conditions, predominantly during the incubation stage, affects offspring survival and body condition at independence. During most of the incubation period, warm sea surface temperatures were correlated with low hatching success, while rainfall in the middle of the incubation stage was correlated with high fledging success. In addition, chicks from nests that experienced warm sea surface temperatures from the pre-laying stage to near-fledging had lower body condition at 70 days of age. Finally, we show that variable annual SST conditions before and during the incubation stage can impair breeding performance. Our results provide insight into how seasonal and interannual weather variation during key reproductive stages can affect hatching success, fledging success, and fledgling body condition in a long-lived neotropical seabird.

Keywords Shifting environments, weather effects · Long-term monitoring · Neotropical · Seabird · Breeding success · Weather conditions · Asynchronous reproduction

Introduction

Along with the alarming trend of increasing global temperatures, several climatic models project more variable climatic conditions, particularly in (sub)tropical regions (Corlett 2012; Thornton et al. 2014; Bathiany et al. 2018; Kusunoki et al. 2020), along with more extreme weather events (Stott 2016). By increasing the frequency of reproductive failure or reducing nestling and adult survival, both seasonal and intraannual weather variations can potentially influence avian population dynamics (Moreno and Møller 2011).

Breeding investment and success of avian species are strongly influenced by weather conditions at the breeding grounds (Forchhammer et al. 1998). Weather can affect avian reproduction either directly, for example through nest flooding due to rainfall (Simeone et al. 2002), or indirectly, for example by altering food availability (Shutt et al. 2019). To date, most studies have focused on how changes in winter and spring temperatures affect the timing of reproduction (Parmesan and Yohe 2003) and clutch size, the latter often being strongly associated with phenology in North temperate species (Dunn 2019). Indeed, short-term empirical and experimental studies have shed light on how changes in weather conditions during the breeding season can affect breeding performance (e.g., Bordjan and Tome 2014; Rodríguez and Barba 2016). However, little is known about how weather variability over the course of the reproductive season can affect birds' breeding success, particularly that of species with a slower pace of life (long lifespan, low reproductive rate and slow-developing offspring; Gaillard et al. 1989).

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It is well documented that some birds can modify the timing of reproduction to avoid unfavourable conditions and even match their food phenology (Charmantier and Gienapp 2014; Glądalski et al. 2018). However, they cannot escape weather changes arising during parental care. In consequence, there is growing interest in studying how weather variability during the incubation and brood care stages affects offspring development and survival (for example, Southern Pied Babbler *Turdoides bicolor* (Bourne et al. 2021); Black-legged kittiwake *Rissa tridactyla* (Christensen-Dalsgaard et al. 2018; Sauve et al. 2022); Great tit *Parus major* (Marques-Santos and Dingemanse 2020)).

Intra-annual weather variability can increase offspring mortality. For example, in the great tit, a short-lived passerine which adjusts its laying date to air temperature (Charmantier et al. 2008), fluctuations both in air temperature and rainfall during brood care –but not during incubation– have been linked to nestling survival and body condition (Marques-Santos and Dingemanse 2020). Specifically, low minimum temperatures and high mean rainfall depressed hatchling survival while low maximum temperatures diminished nestling mass, presumably because low temperatures depress food availability and rain chills nestlings (Marques-Santos and Dingemanse 2020). In the White stork (*Ciconia ciconia*), a long-lived bird that also modifies its laying date in response to weather conditions as follows: nests exposed to low minimum temperatures during incubation had lower hatching success, probably because cold temperatures affect embryonic development (Tobolka et al. 2015). It follows that by exposing offspring to different weather conditions within the same reproductive season, for example, experiencing low temperatures during the incubation stage followed by more benign conditions during the brood care stage, weather variability can alter a population's demography. Therefore, there is an urgent need to understand how organisms respond to intra-annual climate variability, particularly in declining populations with long rearing periods, such as those of seabirds (Lescroël et al. 2016).

Here we implemented the "critical time window" approach to investigate when and whether local sea surface temperatures (SST; a proxy of food availability) and rainfall during the breeding season of the Blue-footed booby (*Sula nebouxii*), a neotropical seabird, affect hatching success, fledging success, and offspring body condition at fledging. These socially monogamous seabirds are faithful to the vicinity of their first nesting site (Osorio-Beristain and Drummond 1998; Kim et al. 2007) and mainly feed on small pelagic fish (Ancona et al. 2012; González-Medina et al. 2018). As SST rises, this booby's most common prey are less abundant and move northwards (Morales-Bojórquez et al. 2003; Lluch-Cota et al. 2017); hence we expect that nests which experience low food availability during the pre-laying, incubation, and brood care stages will hatch fewer eggs,

fledge fewer chicks, and produce fledglings with poorer body condition than those experiencing high food availability in those stages. Similarly, we predict a detrimental effect of rainfall on hatching success, fledging success, and fledgling body condition when experienced during incubation and/or in the first weeks of rearing. Rainfall can increase the probability of eggs and nestlings dying of exposure, reduce foraging efficiency of the parents—leading to nestling starvation—flooding of the nests—which blue-footed boobies lay on the ground (Nelson 1978)—or even lead to nest abandonment (Bionda and Brambilla 2012; Anctil et al. 2014).

Finally, as persistent weather patterns can lead to extreme weather events (e.g., droughts, floods, and heat waves; Francis and Vavrus 2012) such as persistent El Niño-like warm waters in the area around Isla Isabel, we tested whether years with more variable SSTs and rainfall hatched more eggs, fledged more chicks, and raised fledgings with higher body condition than less variable years.

Materials and methods

Study population

Blue-footed boobies of Isla Isabel, Nayarit, Mexico (21.849722° N, 105.881667° W), start reproduction between their first and twelfth years (Drummond et al. 2011) and can live up to 25 years (Ortega et al. 2017). After a courtship period—which lasts ~1–4 weeks (Osorio-Beristain and Drummond 1998)—,female boobies lay 1–3 eggs per nest at ~5-day intervals. Both parents share all parental duties from incubation (which lasts 40.45 ± 0.76 days, mean ± S.D.) through chick fledging (~70 days old). The reproductive phenology of the population on Isla Isabel is highly asynchronous (Fig. 1): laying of the first egg follows a bimodal pattern between November and July (peaking at mid-December and late-March), hatching of the first egg occurs between mid-December and early July (peaking between late-January and early-March), and fledging of the first chick happens from late-February to mid-August (peaking in mid-April). However, hatching and fledging dates are unimodal since most eggs laid during the second peak (late-March) are lost to seagull predation during the first 5 days of incubation (Mayani-Parás et al. 2015) and to milk snake predation on hatchlings (Ortega et al. 2021).

On Isla Isabel, two indices of coupled ocean–atmosphere dynamics correlate with yearly average reproductive success of nesting pairs: the sea surface temperature (SST) anomaly at a 111 km × 111 km grid centred 55 km southeast of Isla Isabel (21.501365° N, − 105.499978° W) and the Southern Oscillation index (SOI) (Ancona et al. 2011). SST anomalies are departures from the average temperature during the same month in a 30-year reference period (1971–2000; Reynolds
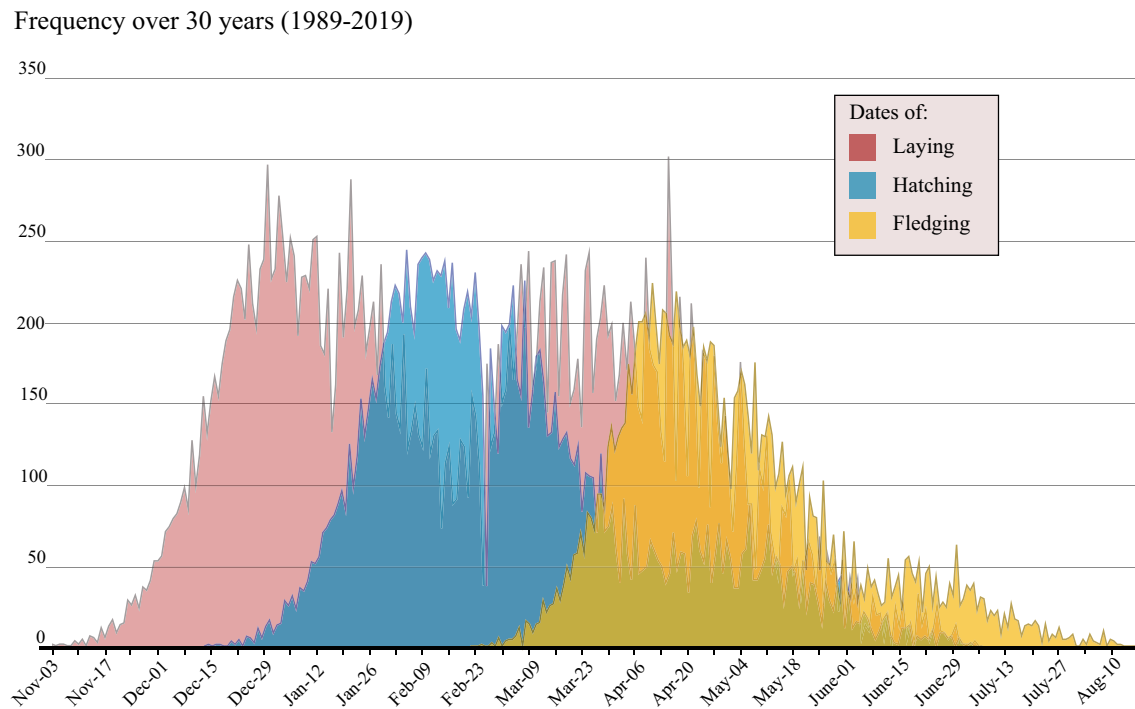
Frequency over 30 years (1989-2019)

Fig. 1 Breeding phenology of the blue-footed booby on Isla Isabel. Dates of 29,147 first laid eggs, 16,255 hatched eggs, and 12,422 fledged chicks across 31 reproductive seasons from 1989 to 2019

et al. 2002; Xue et al. 2003); they are positive when SSTs are warmer than average. SOI measures the difference in surface air pressure between Tahiti and Darwin, Australia; values are negative when trade winds weaken, and SST rises in the eastern tropical Pacific (Hastenrath 2015). In the booby population, for every positive one-degree deviation from the 30-year February mean, the population's average hatching success (total number of chicks divided by total number of eggs), is reduced by 16%, presumably as ocean productivity in the north Pacific declines with warm waters (Dunstan et al. 2018). For every one-unit decrease in mean SOI values during December–March, the population's mean fledging success (total number of fledglings divided by total number of chicks) is depressed by 7%.

Demographic data

Between 1989 and 2019, demographic data were collected during lifetime annual monitoring of individual blue-footed boobies on Isla Isabel (Drummond et al. 2003; Kim et al. 2007). Throughout each breeding season (~ February–July but it can start as early as November and end as late as August; unpublished data), the nest contents of all breeding pairs breeding in two study areas were recorded every 3–6 days from the onset of the incubation period through fledging. The intermediate date between the previous survey and the first time the egg (hatchling) is seen, is assigned as its laying (hatching) date. Clutch sizes of all nests established before the start of the field season are registered during the first nest survey and their laying dates are estimated from their hatching dates. At 70 days, a proxy of fledging age, individuals were individually banded with alphanumeric steel rings.

Weather data

Daily average values of both sea surface temperature (SST) and rainfall used in this study were derived from the NOAA/NASA' AVHRR Pathfinder SST (v.5.3; available at https://catalog.data.gov/dataset/avhrr-pathfinder-version-5-3-level-3-collated-l3c-global-4km-sea-surface-temperature) and the UCSB's CHIRPS (v2.0; Funk et al. 2015; available at https://data.chc.ucsb.edu/products/CHIRPS-2.0/), respectively, for the period 1988–2019. Grid size for SST (~ 60 × 52 km) was based on the foraging range of this species on Isla San Ildefonso in the Gulf of California, Mexico and on Isla Lobos de Tierra, Peru, (~ 30 km; Zavalaga et al. 2008; Weimerskirch et al. 2009) and was centred ~ 5 km west of Isla Isabel. Grid size for rainfall (~ 5 × 5 km) encompassed the north side of the island and was centred ~ 3 km northeast of it.

Statistical analyses

Before implementing the "critical time window" approach, we first built the following three base models: two binomial generalized linear mixed models with a logit link function and a linear mixed model with an identity link function that accounted for differences in: (1) hatching success, (2) fledging success, and (3) fledgling body condition, correspondingly. Hatching success and fledging success were the proportions of eggs and chicks in every nest that hatched and fledged, respectively. For every offspring, we estimated its body condition at fledging (body mass corrected for size at 70 days-old) by taking the residuals from the linear regression of log-transformed body mass (g) on ulna length (mm) (c.f. McLean et al. 2018). All base models included clutch size or brood size as three-level categorical variables. The fixed effects accounted for the initial reproductive investment in either incubation (clutch size) or rearing (brood size). Year, female identity, and male identity were added as random effects to account for statistical non-independence. Chick rank (a three-level category) was added as a fixed effect to the fledgling body condition base model to control for possible differences in body size related to their hatching order (Drummond et al. 1991), and nest number was also included but as a random effect, as siblings, which are statistically non-independent, may be included in the sample.

Only nests for which parental identity was known were included in the sample, and those that were manipulated for other studies, re-nesting attempts (i.e., when a pair establishes a second nest within the same season) and clutch sizes bigger than three were excluded (only ~ 0.001% of pairs produce more than 3 eggs), leaving samples of 2441 and 966 nests for analysis of hatching and fledging success, respectively. For 26 reproductive years, mean ($\pm$ S.D.) clutch size and brood size were 1.96 ± 0.48 eggs and 1.63 ± 0.58 chicks, correspondingly. To analyse body condition, the sample included 507 fledglings from 409 nests for which body mass and ulna length were available. For 21 reproductive years, mean weight, and ulna length at 70 days were 1477.65 ± 274.47 g and 201.27 ± 12.95 mm, respectively.

All analyses were performed in the R statistical environment (R Development Core Team 2020). All independent variables were standardized prior to model fitting to facilitate the interpretation of parameter estimates (Grueber et al. 2011; Cade 2015). Variable standardization was carried out using the *rescale* function in the R package *arm* (Gelman et al. 2016). We used the *glmer* function in the *lme4* package (Bates et al. 2014) to build generalized linear mixed models (GLMMs).

Critical time windows

We used the *slidingwin* function from the *climwin* package (Bailey and De Pol 2016; van de Pol et al. 2016) to search for critical windows, i.e., the weather time periods that predicted for every nest its as follows: (1) hatching success, and (2) fledging success, and for every fledgling, (3) its body condition at 70 days. This sliding window approach allows simultaneously testing for relevant time periods, the best descriptive metric (e.g., mean, max, min), and the function (e.g., linear, quadratic) that best describes the relationship between the weather and the biological response (Hidalgo Aranzamendi et al. 2019). Given the asynchrony of this population's nesting (Fig. 1), the tests were set to search for the time windows of each nest or fledgling. The start of the pre-laying period (~ 1 month before laying the first egg) was used the reference starting point for the window ranges of all analyses. Ten weeks (~ the pre-laying period plus the mean incubation period in this population) were used as ending reference for hatching success. For fledging success and fledgling body condition, 20 weeks (~ 4 weeks of the pre-laying period plus the entire early development period) were used as their ending reference.

To find the best-supported model, *climwin* compares the AICc of each model relative to the base model (i.e., a model with no weather signal). For each window search, we selected the best-supported model based on its ΔAICc (the model with the lowest value) (Burnham and Anderson 2004). If several models had similar AICc values, the most parsimonious model (i.e., with the smaller number of parameters) was selected. To determine whether an observed weather signal did not occur by chance (a false positive), we compared the distribution of ΔAICc values of the best-supported model in 50 randomized data sets with no weather signals with the ΔAICc value of the best supported model in the observed data set (van de Pol et al. 2016). For this study, we considered a signal to be reliable when $P_C < 0.05$; P_C values denote the probability that the climate signal is a false positive. The summary of all tested sets of climate window parameters are provided in Table S1 of the Electronic Supplementary Material.

When signals for SST and rainfall were simultaneously detected and equally supported for any dependent variable, the correlation between critical windows was estimated. If the critical windows for both weather conditions temporarily overlapped, we used the *crosswin* function to measure the correlation between each of the intersecting weeks, and a Pearson's correlation was instead estimated if the critical windows did not overlap. If the variables were not found to be moderately or strongly correlated (a correlation coefficient between 0.30–0.49 or 0.50–1, respectively), we added the best-supported window of one of the two weather variables to the base model of

the other weather variable, and vice versa, and re-ran all the window searches (Electronic Supplementary Material Table S1). This process allowed us to test whether the second weather signal remains supported after accounting for the weather signal of the first best-supported model (van de Pol et al. 2016; Hidalgo Aranzamendi et al. 2019). If the opposite occurred, and the weather variables were correlated, a single model, the one with the lowest AICc value was chosen.

Intra-annual weather variability

We built two binomial linear models with a logit link function and a linear model with an identity link function to evaluate whether years with more variable weather had higher mean hatching success (number of chicks/number of eggs) and fledging success (number of fledglings/number of chicks), and produced, on average, fledglings with a higher body condition than less variable years. For every climatic window, we extracted its weather values and calculated their yearly robust coefficient of variation based on the median (RCV_M; Arachchige et al. 2022), an expression of each window's relative variability. Each model included the RCV_Ms of its previously selected climatic windows as fixed effects. The robust coefficient of variation based on the median is as follows:

$$RCV_M = \left(1.4826 \times \frac{MAD}{m}\right) \times 100,$$

where MAD $(m|x_i - m|)$ and m denote the median absolute deviation and the median, respectively. Note that the

multiplier 1.4826 represents the quantile function for the $N(0,1)$ distribution (Arachchige et al. 2022).

Bayesian framework

Using the data from the best-supported models, we incorporated weakly informative priors into the analyses to constrain the estimated effect sizes to believable values and to prevent erroneous estimation of large effect sizes (Lemoine et al. 2016). Fixed effects were given a normal prior of $N(0,1)$, which indicates that we expect most responses to be within one standard deviation of the response and that large effects should be relatively rare (Lemoine et al. 2016). The random effects were given the default LKJ distribution as prior (which is used to control the expected amount of correlation among the parameters; Gabry et al. 2020; Stan Development Team 2022). The posterior distributions of the parameters along with their 89% highest posterior density intervals were drawn by running five randomly initialized Markov chains, each for 10,000 iterations (which included a warmup period of 1000 iterations that is discarded). All models and posterior predictive checks were run using the packages *rstanarm* (Gabry et al. 2020) and *shinystan* (Gabry et al. 2018), respectively.

Results

Weather conditions around Isla Isabel

From 1988 to 2019, mean SST in the waters surrounding Isla Isabel progressively decreased from 28.21 ± 1.38 °C

Fig. 2 Weather conditions on Isla Isabel and its surrounding waters (1988–2019)
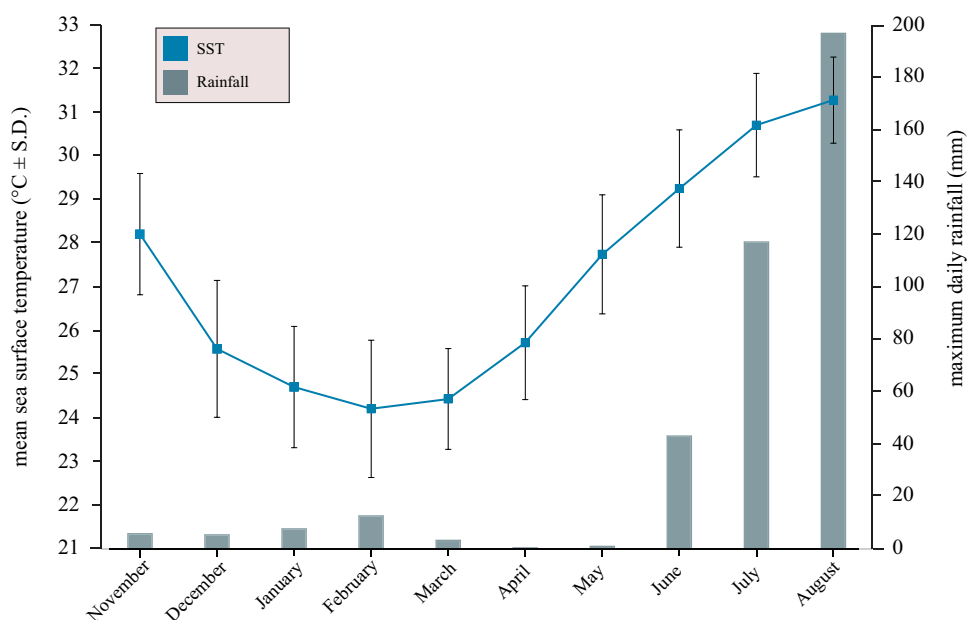
(mean ± standard deviation) in November to 24.21 ± 1.57 °C in February and then gradually increased to 31.28 ± 0.98 °C in August (Fig. 2). Maximum daily rainfall during the boobies' reproductive season also varied, with a marked rainy season between June and August (range 43.10–196.82 mm; Fig. 2). August, with the highest rainfall, is also the start of the hurricane season—which extends up to early November (CONANP 2005). April and May were the driest months, with maximum daily rainfall of < 1 mm.

Hatching success

For 2441 incubated clutches, only sea surface temperature explained variation in the proportion of eggs that hatched. Mean SST between the First week of each pair's pre-laying period and their fifth week of incubation—a week prior to hatching—(Electronic Supplementary Material Table S1a; Fig. 3a) affected hatching success in a nonlinear manner (Table 1a, Fig. 3b). The proportion of eggs that hatched was roughly 37% when mean SST was 21.5 °C, increasing up to 44% between 22.5 and 24.5 °C and then progressively

declined to 3% at > 29.5 °C (Fig. 3b). Hatching success was found to differ with clutch size (Table 1): clutches of three and two eggs hatched a higher proportion of eggs than one egg-clutches (median; 48%, 54%, 37%, respectively; Table 1). Furthermore, SST conditions experienced by each pair were found to be strongly and positively correlated with their mean Julian lay date (each nests' mean laying date transformed into their corresponding Julian date, with November 6th set as day 1) as follows: later breeders experience warmer mean SSTs (Pearson's correlation: $r = 0.76$, $p = < 0.00$).

Fledging success

For 966 broods, the proportion of hatchlings that fledged was explained by rainfall but not by SST. Minimum rainfall between the second and fourth week of each pair's incubation (Table S1b, Fig. 3a) positively affected their fledging success (Table 2, Fig. 3c). Fledging success progressively increased from 55% at ~0 mm of rain up to ~87% between 16 and 24 mm of rain. Fledging success was also affected by
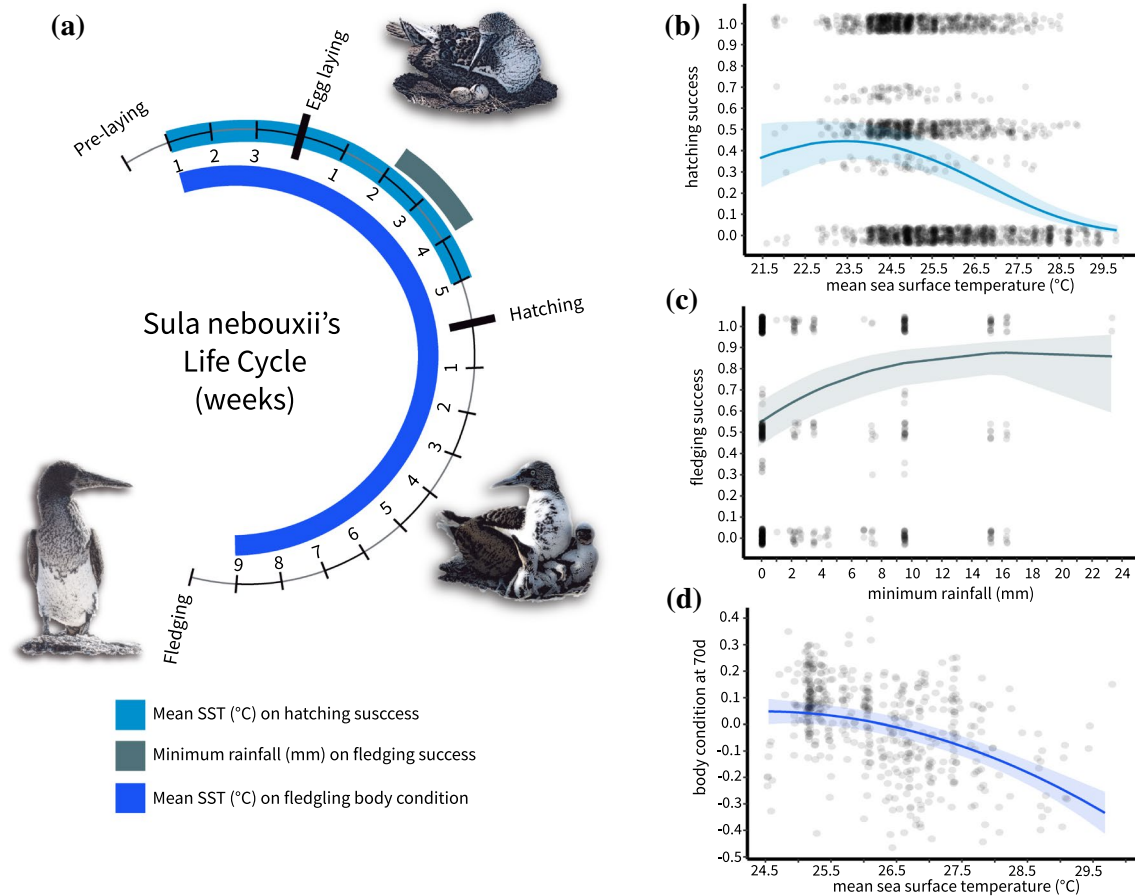

Fig. 3 a Critical time windows of SST and rainfall during the boobies' reproduction. Effects of b mean SST on hatching success, c minimum rainfall on fledging success, and d mean SST on fledgling body condition. Median effects of each weather condition and their 89% highest posterior density intervals are presented as shaded areas; dots are raw observations

Table 1 Weather effects on the proportion of eggs that hatched in 2441 incubated clutches

Parameter	Median	89% HPD	MAD Std. Dev
Intercept	**− 0.520**	**[− 0.865, − 0.192]**	**0.20**
Mean SST	**− 0.878**	**[− 1.048, − 0.697]**	**0.10**
Mean SST^2	**− 0.636**	**[− 0.898, − 0.380]**	**0.20**
Clutch size[a]			
2	**0.681**	**[0.418. 0.913]**	**0.20**
3	**0.446**	**[0.157, 0.745]**	**0.20**

Random effects	Std. Dev.		n
Male ID	0.93		1450
Female ID	0.65		1306
Year	0.63		26

Terms whose highest posterior density (HPD) intervals did not contain zero are presented in boldface type. Median absolute deviations (MAD) from the standard deviation are provided

[a]Clutches of one egg were used as reference level

Table 2 Effect of minimum rainfall on the proportion of chicks that fledged in 966 broods

Parameter	Median	89% HPD	MAD Std. Dev
Intercept	**0.588**	**[0.144, 1.008]**	**0.30**
Minimum rainfall	**1.510**	**[0.910, 2.075]**	**0.40**
Minimum rainfall^2	− 0.438	[− 0.866, 0.005]	0.30
Brood size[a]			
2	**− 0.691**	**[− 0.915, − 0.472]**	**0.10**
3	**− 0.898**	**[− 1.262, − 0.546]**	**0.20**

Random effects	Std. Dev.		n
Male ID	0.58		756
Female ID	0.37		729
Year	1.07		26

Parameters whose highest posterior density (HPD) intervals did not contain zero are presented in boldface type

MAD median absolute deviation

[a]Nests rearing only one chick were used as reference level

brood size as follows: one chick broods were more successful than broods of two and three chicks (64%, 47% and 42%, respectively; Table 2). Furthermore, minimum rainfall during each pairs' incubation stage was strongly and negatively correlated with their mean Julian lay day as follows: late breeders experienced drier conditions (Pearson's correlation: $r = − 0.58$, $p < 0.00$).

Fledgling body condition

Body condition of 507 fledglings from 409 nests correlated only with SST. Mean SST between the first week of the pre-laying period and the 9th week of rearing—a week before reaching 70 days—(Table S1c; Fig. 3a) negatively affected fledgling body condition in a non-linear way. Fledgling body condition was 0.06 at 24.5 °C and progressively declined to − 0.37 at > 29.5 °C (Table 3, Fig. 3c). First-hatched fledglings had a higher body condition than second- and third-hatched fledglings (− 0.02, − 0.05, − 0.17, respectively; Table 3). Similarly, fledglings from broods of three and two chicks had a lower body condition than broods of one (− 0.14, − 0.06, and − 0.04, respectively; Table 3). In addition, mean SST experienced by each pair during most of their reproduction (their best-supported critical window) was found to be strongly and positively correlated with each pairs' mean Julian lay date as follows: chicks of late breeders experienced warmer SST conditions throughout their early development (Pearson's correlation: $r = 0.77$, $p < 0.00$).

Table 3 Effect of mean SST on the body condition of 507 fledglings

Parameter	Median	89% HPD
Intercept	0.008	[− 0.031, 0.049]
Mean SST	**− 0.108**	**[− 0.135, − 0.080]**
Mean SST^2	**− 0.063**	**[− 0.098, − 0.028]**
Rank[a]		
2nd	**− 0.025**	**[− 0.042, − 0.006]**
3rd	**− 0.146**	**[− 0.214, − 0.076]**
Brood size[b]		
2	**− 0.021**	**[− 0.040, − 0.002]**
3	**− 0.093**	**[− 0.145, − 0.042]**
Random effects	Std. Dev.	n
Male ID	0.04	365
Female ID	0.03	357
Nest ID	0.03	409
Year	0.09	21

Terms whose highest posterior density (HPD) intervals did not contain zero are presented in boldface type. Median absolute deviations from the standard deviation for all terms were < 0.0

[a]First hatched chicks

[b]Nests rearing only one chick were used as reference levels

Intra-annual weather variability

For 26 years, the average proportions of eggs that hatched and chicks that fledged were 0.46 ± 0.42 and 0.48 ± 0.43 (mean $\pm$ S.D.), respectively, and the average body condition for 21 years was 0.00 ± 0.15. Annual robust coefficient of variation (RCV_M) of the average SST experienced by each pair between their 1st week pre-laying period and their 5th week of incubation was negatively correlated with annual hatching success (Table 4a). Annual hatching success was 53% and 23% for the years with the most stable and most variable SSTs, respectively. Neither yearly fledging success nor average fledgling body condition

was explained by the RCV_Ms of minimum rainfall and mean SST, respectively (Table 4b, c).

Discussion

We examined the effects of shifting weather conditions within the breeding season on blue-footed booby offspring survival and body condition at fledging—which is critical for fitness after fledging in birds (Morrison et al. 2009). We show that, depending on the reproductive stage when they occur, weather conditions can affect annual breeding parameters. Specifically, under high SST fewer eggs hatch, with

Table 4 Effects of intra-annual variability on yearly: (a) hatching success, (b) fledging success, and (c) fledgling body condition

Parameter	Median	89% HPD	MAD	Range of CVs
Hatching success ($n = 26$ years)				
Intercept	− 0.158	[− 0.224, − 0.093]	0.00	–
Mean SST RCV_M	**− 0.539**	**[− 0.745, − 0.332]**	**0.10**	**0.06–16.84%**
Fledging success ($n = 26$ years)				
Intercept	− 0.046	[− 0.159, 0.070]	0.10	–
Minimum rainfall RCV_M	− 0.096	[− 0.224, 0.027]	0.10	0–132.43%
Fledgling body condition ($n = 21$ years)				
Intercept	− 0.030	[− 0.075, 0.013]	0.00	–
Mean SST RCV_M	− 0.007	[− 0.096, 0.083]	0.10	0–7.41%

Left column shows the effect of the coefficient of variation of the yearly weather conditions' critical time windows. For every weather condition, the range of coefficient variation is reported in the right column. Parameters whose highest posterior density (HPD) intervals did not contain zero are presented in boldface type. Median absolute deviation (MAD) for each parameter is provided

high levels of rainfall more chicks fledge, and when reared under high SST, chicks fledge with lower body condition. Finally, we show that years with high SST variability have lower hatching success than years with more stable weather conditions.

Hatching success

Mean SST (a proxy of food availability) between the first week of each blue-footed booby pair's pre-laying period and their fifth week of incubation—a week before hatching—was correlated with hatching success. Within this time window, mean SST values greater than 24.5 °C, when food is likely to be scarce, triggered a reduction in the proportion of eggs that hatched. This pattern is consistent with the finding that anomalously warm waters south-east of Isla Isabel in February negatively affect the hatching success of the study population (Ancona et al. 2011). It complements that earlier result by shifting the focus away from an interannual deviation from a base period in the North Pacific onto the weather conditions experienced by individuals in situ, and by delimiting the window of vulnerability to warm SST. Interestingly, a detrimental—albeit small—effect of low mean SSTs (< 21.5 °C) near Isla Isabel on hatching success was detected. The slight reduction in hatching success may also be a result of low food availability as follows: phytoplankton blooms—the sustenance of the boobies' preys—are known to require warming of the water for them to occur (Trombetta et al. 2019).

SST could influence hatching success in the following two ways: by affecting food availability and thence adult body condition, or by providing parents with a cue to upcoming food availability for hatchlings and thereby affecting their investment decisions. According to life-history theory, long-lived iteroparous species are expected to assign their finite supply of resources in a way that allows them to evade or mitigate the impacts of stressful environments on adult survival—the parameter with greatest impact on their lifetime fitness (Gaillard and Yoccoz 2003; Boyce et al. 2006). Confronted with low food availability before and during incubation, blue-footed boobies may lower their current reproductive investment, as do wood ducks (*Aix sponsa*; Hepp et al. 2005) and tree swallows (*Tachycineta bicolor*; Pérez et al. 2008), for example, by defending clutches less vigorously against seagulls or even abandoning them.

Fledging success and fledgling body condition

The occurrence of rainfall during the second to fourth weeks of incubation increased the proportion of chicks that fledged while high mean SSTs present during the first week of the pre-laying period to the ninth week of rearing decreased the body condition of the offspring at fledging. Here again,

rainfall and SST may function as cues to future availability of food for fledglings and elicit changes in parental investment, with investment increasing when it rains and decreasing when SSTs are high. Rainfall increases chlorophyte abundance in coastal seas (Thompson et al. 2015) because atmospheric nutrient input and river-delivered nutrients increase with rain (e.g., Kim et al. 2014). This increase in ocean productivity leads, in turn, to an increase in the abundance of the engraulids (i.e., anchovies) and clupeids (i.e., sardines and herrings) that blue-footed boobies—most commonly—prey on. Rainfall near the middle of the incubation stage could stimulate parents to increase nest attendance (e.g., Fu et al. 2017; de Zwaan et al. 2020) and foraging to support growth of the soon-to-hatch nestlings, thus increasing their survival. The adverse effect of scarce rainfall on each pair's fledging success is consistent with the previously reported effect of negative SOI values (in December–March) on the yearly average fledging success of this population (Ancona et al. 2011): negative SOI values have been associated with below average rainfall (Stone and Auliciems 1992).

On the other hand, warm SSTs throughout most reproductive stages can signal both present and future food shortage, a scenario under which parental investment is expected to decrease in preparation for future reproduction. This pattern occurs in common fiscals *Lanius collaris* (Cunningham et al. 2013), pied babblers *Turdoides bicolor* (Wiley and Ridley 2016), and tree swallows (Tapper et al. 2020), resulting in lower provisioning rates or even the allocation of poor-quality food to the young—that is, low-lipid food (González-Medina et al. 2018)—which ultimately leads to offspring fledging with low body condition. A long-term study on a temperate marine bird, the black-legged kittiwake (*Rissa triadctyla*), showed a similar pattern as follows: low abundance of its preferred prey during the rearing stage impaired nestling growth (Sauve et al. 2022). To explore this idea, measures of body condition of both booby adults and their offspring during their reproductive and early development stages will be needed, along with data on prey abundance.

As the breeding season progresses, breeders are exposed to drier and warmer SST conditions, which, in turn, can lead them to lower their current reproductive investment (this study) and, ultimately, generate the unimodal nature of both the hatching and fledging phenology—in contrast with the bimodal distribution on laying dates—in this population (Fig. 1). In Southwest Mexico, during El Niño events, characterized by negative SOI values, the correlation between rainfall and negative SOI values may be strengthened, leading to a deficit of rain in May–October (Magaña et al. 2003; Bravo-Cabrera et al. 2017). El Niño-induced reduction in rainfall could impose a greater challenge to late breeders. However, what happens during an El Niño event does not affect our overall interpretation since blue-footed boobies

tend to skip reproduction when strong El Niño events develop before and during the breeding season. For example, fewer than 30 breeding pairs tried to reproduce on the island during the events of 1992 and 2016 (unpublished data).

Intra-annual weather variability

Contrary to expectation, years with more stable mean SSTs before and during the incubation stage of each breeding pair were more successful than years in which pairs experienced more variable SSTs during this time window. Relatively stable SSTs —which are negatively correlated with wind speed (Wang et al. 1999)—may function as a reliable cue to future food availability. Cool and stable SSTs before hatching may engender/facilitate the natural cycle of primary productivity (Chavez et al. 2011) as follows: the accumulation of nutrients that upwell when SSTs are cold and wind speeds are high. As the breeding season progresses and SSTs increase, the accumulation of nutrients during the first stages of reproduction may trigger phytoplankton blooms—which can occur between 0 and 5 days after an increase in SST (Trombetta et al. 2019)— attracting and nourishing prey. We found weak and inconclusive evidence of the effects of yearly rainfall variability on fledging success. The inconclusiveness of this finding might be due to the outstanding range of minimum rainfall RCV_Ms, which may be due to seasonal weather patterns: rains accompanying the end of the hurricane season, which ends in November (CONANP 2005). In contrast, the restrictive range of minimum SST RCV_Ms might explain the inconclusiveness of their negative effect on fledgling body condition. Blue-footed boobies may raise fledglings only when mean SSTs are relatively stable, but more morphological and yearly data are needed to confirm this.

Here we showed for a population of blue-footed boobies off the Pacific Coast of Mexico that offspring survival and condition at independence vary in function of the weather conditions experienced by each pair' during key reproductive stages. In response to weather conditions before and after laying, these long-lived birds may optimize their fitness by strategically modulating their parental investment. Climate variation in the tropics is predicted to increase with climate change (Williams et al. 2007; Corlett 2012), potentially altering the abundance, distribution and phenology of seabirds' prey species (e.g., Ancona et al. 2012; de Zwaan et al. 2020) and, ultimately, affecting the population dynamics of seabirds. Our results provide some insight into how wild populations may respond to unpredictable weather variations during their reproduction. Nevertheless, direct behavioural observations are needed to evaluate the regulatory mechanisms we tentatively infer, along with analyses of the potential payoffs of reducing current reproductive investment. Research also needs to focus on how weather conditions affect the adult phenotype of surviving offspring. More research on how tropical species respond to variable weather conditions will be essential to predict the impacts of climate change within the biodiversity hotspot that is the tropics.

Availability of data and materials All data from this study are provided in the electronic supplementary material.

Code availability All scripts supporting this article have been uploaded as part of the electronic supplementary material.

Declarations

Conflict of interest Authors have no conflicts or competing of interests to declare.

Ethics approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed. The Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) provided the permits for fieldwork. Last 5 permits are stated: SGPA/DGVS/07035/20; SGPA/DFVS/00422/19; DGPA/DGVS/012166/17; SGPA/DGVS/19273/17; SGPA/DGVS/11084/16.

Consent to participate Not applicable.

Consent for publication Not applicable.

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