

Weather effects on offspring survival differ between reproductive stages in a Neotropical seabird.

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1 **Weather effects on offspring survival differ between reproductive stages in a**
2 **Neotropical seabird.**

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10 **Abstract**

11 Weather conditions can profoundly affect avian reproduction. Thus far, most studies on
12 weather effects have focused on how weather conditions prior to clutch initiation affect
13 laying dates and, ultimately, breeding success. By contrast, little is known of how weather
14 conditions after the onset of reproduction affect birds. Using a 32-year population study of
15 the Blue-footed booby (*Sula nebouxii*) in Mexico, we show that effects of weather
16 conditions on offspring survival and body condition at independence vary with the
17 reproductive stage at which they occur. During most of the incubation period, warm sea
18 surface temperatures and low to moderate rainfall depressed hatching success; while during
19 the last month of brood care surface temperatures were unimportant but rainfall increased
20 fledging success. In addition, chicks that experienced warm sea surface temperatures in the
21 middle of the brood care stage had lower body condition at fledging. Our results provide
22 insight of how weather effects vary between reproductive stages in a long-lived neotropical
23 seabird.

24 **Keywords:** weather effects; neotropical; seabird; breeding success; weather conditions

25

26 **Introduction**

27 Along with the alarming trend of increasing global temperatures, several climatic models
28 project more variable climatic conditions, particularly in (sub)tropical regions (Corlett
29 2012; Thornton et al. 2014; Bathiany et al. 2018; Kusunoki et al. 2020), which, in turn, may
30 increase the magnitude and occurrence of extreme weather events (Stott 2016). By
31 increasing the frequency of reproductive failure or reducing adult survival, intra-annual
32 weather variations have the potential of influencing bird population dynamics (Moreno and
33 MØller 2011).

34 Breeding investment and success of avian species are strongly influenced by weather
35 conditions at the breeding grounds (Forchhammer et al. 1998). Weather can affect avian
36 reproduction either directly, for example through nest flooding due to rainfall (Simeone et
37 al. 2002), or indirectly, for example by altering food availability (Shutt et al. 2019). To
38 date, most studies have focused on how changes in winter and spring temperatures affect
39 the timing of reproduction (Parmesan and Yohe 2003) and clutch size, the latter being often
40 and strongly associated with phenology in North temperate species (Dunn 2019). In
41 contrast, little is known of how changes in weather conditions during the breeding season
42 can affect other reproductive traits and, ultimately, fitness.

43 It is well documented that some birds can modify the timing of reproduction to avoid
44 unfavourable conditions and even match their food phenology (Charmantier and Gienapp
45 2014). However, they cannot escape weather changes arising during parental care. In
46 consequence, there is growing interest in studying how weather variability during the
47 rearing and brood care stages affects offspring development and survival (for example,
48 Southern Pied Babbler *Turdoides bicolor* (Bourne et al. 2021); Black-legged kittiwake

49 *Rissa tridactyla* (Christensen-Dalsgaard et al. 2018); Great tit *Parus major* (Marques-
50 Santos and Dingemanse 2020)).

51 Intra-annual weather variability can increase offspring mortality. For example, in the great
52 tit, which adjusts its laying date to air temperature (Charmantier et al. 2008), fluctuations
53 both in air temperature and rainfall during the brood care stage –but not during incubation–
54 have been linked to nestling survival and body condition. Particularly, low minimum
55 temperatures and high mean rainfall depressed hatchlings’ survival while low maximum
56 temperatures diminished nestlings’ mass, presumably because low temperatures depress
57 food availability and rain chills nestlings (Marques-Santos and Dingemanse 2020). In the
58 White stork (*Ciconia ciconia*), a long-lived bird that also modifies its laying date in
59 response to weather conditions (Tobolka et al. 2018), fluctuations in air temperatures were
60 negatively correlated with offspring survival (Tobolka et al. 2015). Chiefly, nests exposed
61 to low minimum temperatures during incubation had lower hatching success, presumably
62 because cold temperatures affect embryonic development (Tobolka et al. 2015). It follows
63 that by exposing offspring to different weather conditions within the same reproductive
64 season, for example, experiencing low temperatures during the incubation stage followed
65 by more benign conditions during the brood care stage, weather variability can alter a
66 populations demography. Therefore, an urgent need has arisen to understand how
67 organisms respond to intra-annual climate variability, particularly in populations that are
68 already in decline, such as those of seabirds (Lescroël et al. 2016).

69 Here we implemented the “critical time window” approach (van de Pol et al. 2016) to
70 investigate when and whether sea surface temperatures (SST) and rainfall during the
71 breeding season of the Blue-footed booby (*Sula nebouxii*), a neotropical seabird, affect

72 hatching success, fledging success, and offspring body condition at fledging. These socially
73 monogamous seabirds are faithful to their first nesting site (Osorio-Beristain and
74 Drummond 1998; Kim et al. 2007) and mainly feed on small pelagic fish (Ancona et al.
75 2012; González-Medina et al. 2018). As SST rises, this booby's most common prey are less
76 abundant and move northwards (Morales-Bojórquez et al. 2003; Lluch-Cota et al. 2017),
77 hence we expect that nests which experienced high SST during the incubation and brood
78 care stages will hatch less eggs, fledge less chicks, and produce fledglings with poorer body
79 condition than those experiencing cold SSTs in those stages. Similarly, we predict a
80 detrimental effect of rainfall on hatching success, fledging success, and fledgling body
81 condition when experienced during incubation and/or in the first weeks of rearing. Rainfall
82 can increase the probability of eggs and nestlings dying of exposure, reduce foraging
83 efficiency of the parents –leading to nestling starvation–, flooding of the nests –which blue-
84 footed boobies lay on the ground (Nelson 1978)– or even lead to nest abandonment (Bionda
85 and Brambilla 2012; Anctil et al. 2014).

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

91 **Materials and methods**

92 *Study population*

93 Blue-footed boobies of Isla Isabel, Nayarit, Mexico (21.849722°N, 105.881667°W), start
94 reproduction between their first and twelfth years (Drummond et al. 2011), and can live up
95 to 25 years (Ortega et al. 2017). After a courtship period –which lasts ~1-4 weeks (Osorio-
96 Beristain and Drummond 1998)–, female boobies lay 1-3 eggs per nest at 4-day intervals.
97 Both parents share all parental duties from incubation (which lasts 40.45 ± 0.76 days, mean
98 \pm SD) through chick fledging (~70 days old). This population has a highly asynchronous
99 reproductive season (Figure 1): laying of the first egg follows a bimodal pattern between
100 November and July (peaking at mid-December and late-March), hatching of the first egg
101 occurs between mid-December and ends in early-July (peaking between late-January and
102 early-March), and fledging of the first chick happens from late-February to mid-August
103 (peaking in mid-April).

104 Analyses of interannual variation in this population have shown a correlation between the
105 yearly average reproductive success of nesting pairs and two indices of coupled ocean-
106 atmosphere dynamics: the sea surface temperature (SST) anomaly at a 111 km \times 111 km
107 grid centred at 55 km southeast from Isla Isabel (21.501365°N, -105.499978°W) and the
108 Southern Oscillation index (SOI) (Ancona et al. 2011). Anomalies are departures from the
109 average temperature during the same month in a 30-year reference period (1971-2000;
110 Reynolds et al. 2002; Xue et al. 2003); they are positive when SSTs are warmer than
111 average. SOI measures the difference in surface air pressure between Tahiti and Darwin,
112 Australia; values are negative when trade winds weaken, and SST rises in the eastern
113 tropical Pacific (Hastenrath 2015). In this population, for every one-degree deviation from
114 the 30-year February mean SSTAs, average hatching success (total number of chicks
115 divided by total number of eggs), is reduced by 16%, presumably as ocean productivity in

116 the north Pacific declines with warm waters (Dunstan et al. 2018). For every one-unit
117 decrease in mean SOI values during December-March, mean fledging success (total
118 number of fledglings divided by total number of chicks) is depressed by 7%.

119 *Demographic data*

120 Between 1989 and 2019, demographic data were collected during lifetime annual
121 monitoring of individual blue-footed boobies on Isla Isabel (Drummond et al. 2003; Kim et
122 al. 2007). Throughout each field season (~ February-July), the nest contents of all breeding
123 pairs nesting within two study areas were recorded every 3-6 days from the onset of the
124 incubation period through fledging. At fledging (age 70 days), individuals were
125 individually identified by steel bands.

126 *Weather data*

127 Daily average values of both sea surface temperature (SST) and rainfall used in this study
128 were derived from the NOAA/NASA' AVHRR Pathfinder SST (v.5.3; available at
129 [https://catalog.data.gov/dataset/avhrr-pathfinder-version-5-3-level-3-collated-l3c-global-](https://catalog.data.gov/dataset/avhrr-pathfinder-version-5-3-level-3-collated-l3c-global-4km-sea-surface-temperature)
130 [4km-sea-surface-temperature](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
131 at <https://data.chc.ucsb.edu/products/CHIRPS-2.0/>), respectively, for the period 1988-2019.
132 Grid size for SST (~60 x 52 km) was based on the foraging range (~ 30 km; Zavalaga et al.
133 2008; Weimerskirch et al. 2009) of this species on Isla San Ildefonso in the Gulf of
134 California, Mexico and on Isla Lobos de Tierra, Peru, and was centred ~5 km west of Isla
135 Isabel. Grid size for rainfall (~ 5 x 5 km) encompassed the north side of the island and was
136 centred ~3 km northeast of it.

137 *Statistical analyses*

138 We used binomial generalized linear mixed models with a logit link function to evaluate the
139 effect of SST and rainfall on hatching success and fledging success during each nests'
140 incubation and brood care period, respectively. In addition, we built a linear mixed model
141 with an identity link function to assess for the effects of the weather conditions experienced
142 during both reproductive stages on the offspring's body condition at fledging. Hatching
143 success and fledging success were the proportion of eggs and chicks in every nest that
144 hatched and fledged, respectively. For every offspring, we estimated its body condition at
145 fledging (body mass corrected for size at 70d-old) by taking the residuals from the linear
146 regression of body mass (g) on ulna length (mm) (c.f. McLean et al. 2018).

147 To implement the "critical time window" approach, we first selected a base model from a
148 series of candidate models that accounted for differences in 1) hatching success, 2) fledging
149 success, and 3) fledglings' body condition. Fixed variables accounted for a) the initial
150 reproductive investment in either the incubation (clutch size) or the rearing stages (brood
151 size), b) the within seasonal changes in unmeasured environmental conditions (either laying
152 date or hatching date) such as air temperature or increase in the activity of snakes (which
153 prey on newly hatched chicks; Ortega et al. 2021), and c) for age-related changes in
154 breeding success (Velando et al. 2006; Beamonte-Barrientos et al. 2010).

155 All candidate models included laying date or hatching date (Julian date relative to the start
156 of the season) as continuous variables, and clutch size or brood size as three-level
157 categorical variables. Year, female identity and male identity were added as random effects
158 to account for statistical non-independence. Additionally, laying date or hatching date was
159 also included as a random effect because synchronous nests may experience disruptions at
160 the same developmental stages (e.g., floods). Nest number was added as random effect in

161 the fledglings' body condition models as siblings, which are statistically non-independent,
162 may be included in the sample. The linear and quadratic expressions of the progenitors'
163 ages were added separately and together in different candidate models.

164 Nests manipulated for other studies and re-nesting attempts (i.e., when a pair establishes a
165 second nest within the same season) were excluded from the sample, and clutch sizes
166 bigger than three were excluded (only ~0.001% of pairs produce more than 3 eggs), leaving
167 samples of 2441 and 966 nests for analysis of hatching and fledging success, respectively.
168 To analyse body condition, the sample included 511 fledglings from 411 nests for which
169 body mass and ulna length were available.

170 All analyses were performed in the R statistical environment (R Development Core Team
171 2020). All independent variables were standardized prior to model fitting to facilitate the
172 interpretation of parameter estimates (Grueber et al. 2011; Cade 2015). The candidate
173 model with the lowest corrected Akaike information criterion for small samples (AICc) was
174 selected as the best-supported model (Burnham and Anderson 2004). If several models had
175 similar AICc values, the most parsimonious model (i.e., with the smaller number of
176 parameters) was selected. Variable standardization was carried out using the *rescale*
177 function in the R package *arm* (Gelman et al. 2016). We used the *glmer* function in the
178 *lme4* package (Bates et al. 2014) to build generalized linear mixed models (GLMMs).
179 Model selection was carried out with *model.sel* function in the *MuMIn* package (Bartón
180 2016). Model selection tables are provided in the supplementary material (Electronic
181 Supplementary Material Table S1).

182 Critical time windows

183 Once a base model had been selected, we used the *slidinwin* function from the *climwin*
184 package (Bailey and De Pol 2016; van de Pol et al. 2016) to search for critical windows, i.e.
185 the weather time periods that predicted for every nest its 1) hatching success and 2)
186 fledging success, and for every fledgling 3) its body condition and 70d-old. This sliding
187 window approach allows simultaneously testing for relevant time periods, the best
188 descriptive metric (e.g. mean, max. sum), and the function (e.g. linear, quadratic) that best
189 describes the relationship between the weather and the biological response (Hidalgo
190 Aranzamendi et al. 2019). Given the asynchrony of this population's nesting (Figure 1), the
191 tests were set to search for the time windows of each nest or fledglings. Nest average laying
192 date was used as a reference starting point for the window ranges of the hatching success
193 and the fledglings' body condition analyses, while nest average hatching date was used as
194 the starting point for the fledging success analysis. Six weeks of incubation (~ the mean
195 incubation period in this population) and 10 weeks of age (age at fledging) were used as
196 ending reference for hatching and fledging success, respectively. For fledgling body
197 condition, 16 weeks (~the entire early development period) were used as the ending
198 reference. To find the best-supported model, *climwin* compares the AICc of each model
199 relative to the base model (i.e., the previously selected model with no weather signal). For
200 each window search, we selected the best-supported model based on its $\Delta AICc$ (the model
201 with the lowest value) (Burnham and Anderson 2004). To determine whether an observed
202 weather signal did not occur by chance (a false positive), we compared the distribution of
203 $\Delta AICc$ values of the best-supported model in 50 randomized data sets with no weather
204 signals with the $\Delta AICc$ value of the best supported model in the observed data set (van de
205 Pol et al. 2016). For this study, we considered a signal to be reliable when $P_C < 0.05$
206 (Electronic Supplementary Material Table S2); P_C values denote the probability that the

207 climate signal is a false positive. If a signal for SST and rainfall were simultaneously
208 detected for either dependent variable, we added the best-supported window of one of the
209 two weather variables to the base model of the other weather variable, and *vice versa*, and
210 re-ran all the window searches (Electronic Supplementary Material Table S2). This process
211 allowed us to test whether the second weather signal remains supported after accounting for
212 the weather signal of the first best-supported model (van de Pol et al. 2016; Hidalgo
213 Aranzamendi et al. 2019).

214 Intra-annual weather variability

215 We built two binomial linear models with a logit link function and a linear model with an
216 identity link function to evaluate whether years with more variable weather had higher
217 mean hatching success (number of chicks/ number of eggs) and fledging success (number
218 of fledglings/ number of chicks), and produced, on average, fledglings with a higher body
219 condition than less variable years. For every climatic window, we extracted its weather
220 values and calculated their yearly coefficient of variation ($CV = \frac{\sigma}{\bar{x}} * 100$), an expression of
221 each window's relative variability. Each model included the CVs of its previously selected
222 climatic windows as fixed effects.

223 Bayesian framework

224 Using the data from the best-supported models, we incorporated weakly informative priors
225 into the analyses to constrain the estimated effect sizes to believable values and to prevent
226 erroneous estimation of large effect sizes (Lemoine et al. 2016). Fixed effects were given a
227 normal prior of $N(0,1)$, which indicates that we expect most responses to be within one
228 standard deviation of the response and that large effects should be relatively rare (Lemoine

229 et al. 2016). The posterior distributions of the parameters along with their 89% highest
230 posterior density intervals were drawn by running five randomly initialized Markov chains,
231 each for 10000 iterations (which included a warmup period of 1000 iterations that is
232 discarded). All models and posterior predictive checks were run using the packages
233 *rstanarm* (Gabry et al. 2020) and *shinystan* (Gabry et al. 2018), respectively.

234 **Results**

235 Weather conditions on Isla Isabel

236 From 1988 to 2019, mean sea surface temperatures during the booby's reproductive season
237 in the waters surrounding Isla Isabel progressively decreased from 28.21 (± 1.38 ; mean \pm
238 standard deviation) °C to 24.21 (± 1.57) °C between November and February, then
239 gradually increased to 31.28 (± 0.98) °C in August (Figure 2). Maximum daily rainfall also
240 varied within the boobies' reproductive season with a marked rainy season between June
241 and August (range 43.10-196.82 mm; Figure 2). August, with the highest rainfall, is also
242 the start of the hurricane season—which extends up to early-November (CONANP 2005).
243 April and May were the driest months, with maximum daily rainfall of less than 1 mm.

244 Hatching success

245 For 2441 incubated clutches, both sea surface temperature and rainfall explained variation
246 in the proportion of eggs that hatched. Mean SST between the first and fifth weeks of
247 incubation affected hatching success in a nonlinear manner (table 1 and S3, Figure 3a). The
248 proportion of eggs that hatched was roughly 36% at mean SST of 21.2 - 24.5°C, then
249 progressively declined to 0.03% at >30°C (Figure 3b). Minimum rainfall between the
250 second and fifth weeks of incubation (Figure 3a) also had a nonlinear effect on hatching

251 success (Table 1 and S3, Figure 3c). The proportion of eggs that hatched decreased from
252 41% at ~0.0 mm of rain to 33% at 2.95 mm of rain, then increased to 62% at rain levels >
253 9.51 mm (Figure 3c).

254 Hatching success also increased with lateness of laying (Table 1) and clutch size; clutches
255 of three and two eggs hatched a higher proportion of them than one egg-clutches (46%,
256 51%, 35%, respectively; table 1). Mother's age also affected hatching success in a
257 nonlinear way, slightly increasing from 26% at 2 years up to a 34%, plateau at 5 - 12 years,
258 then declining steadily to 9% at age 23 years, confirming a previously reported an inverted-
259 U pattern in this population (Beamonte-Barrientos et al. 2010).

260 Fledging success

261 For 966 broods, the proportion of hatchlings that fledged was explained by rainfall but not
262 by SST. Maximum rainfall during the last 4 weeks of brood care (Table S4, Figure 3a)
263 positively affected fledging success (table 2, Figure 3d). Fledging success linearly
264 increased with rain from 56%, at 0 mm of rain, up to 90% at 85.8 mm of rain. Fledging
265 success was also affected by brood size and hatching date. Broods of three chicks were less
266 successful than broods of one or two chicks (40%, 62% and 45%, respectively; Table 2),
267 and later broods had lower fledging success (Table 2).

268 *Fledgling body condition*

269 Body condition of 411 fledglings at 70 d was unaffected by rainfall but declined with
270 increase in minimum SST between the 5th and 7th weeks of rearing, from 0.11 at 23.2°C
271 down to -0.33 at 29.0°C (Table 3). This window overlapped with the first week of the
272 critical time window for fledging success. Fledglings from broods of three and two chicks

273 had a lower body condition than broods of one (-0.15, -0.10 and -0.07, respectively; Table
274 3). The effect of hatching date on fledglings' body condition was found to be inconclusive
275 (Table 3).

276 Intra-annual weather variability

277 Annual hatching success increased with annual CV of mean SST in the 1st and 5th weeks of
278 incubation but did not improve with the annual CV of minimum rainfall in the 2nd and 6th
279 weeks within the same reproductive stage (Table 4a). Annual hatching success was 28%
280 and 65% for the years with the most stable and most variable SSTs, respectively.
281 Furthermore, years with high SST variability were found to have colder average SST
282 conditions during incubation than more stable years (Spearman correlation: $r_s = -0.37$, $p =$
283 0.05). Neither yearly fledging success nor average fledgling body condition were explained
284 by the CVs of maximum rainfall and minimum SST in the brood care stage, respectively
285 (Table 4b-4c).

286 **Discussion**

287 In general, studies on weather effects have focused on how weather conditions –primarily,
288 temperature– affect the timing of reproduction in temperate birds (Charmantier and
289 Gienapp 2014; Kruuk et al. 2015). Here, instead, we focus on how weather conditions
290 during the incubation and rearing stages of a neotropical seabird (i.e., after initial
291 reproductive decisions have been made) affect offspring survival and body condition at
292 fledging –which is critical for fitness after fledging in birds (Morrison et al. 2009). We
293 show that, depending on the reproductive stage when they occur, weather conditions can
294 differentially affect annual breeding parameters. Specifically, we found that fewer eggs

295 hatch under high SST and low to moderate rainfall, while the latter is associated with
296 increased fledging success, and that chicks reared under high SST fledge with a lower body
297 condition. Finally, we show that years with high SST variability have higher hatching
298 success than years with more stable weather conditions.

299 Hatching success

300 Hatching success of the blue-footed booby was affected by mean SST during most of the
301 incubation period. Within this time window, mean SST values greater than 24.5°C
302 triggered a reduction in the proportion of eggs that hatched. This pattern is consistent with
303 the finding that anomalously warm waters south-east of Isla Isabel in February negatively
304 affect the hatching success of the study population (Ancona et al. 2011). It complements
305 that earlier result by shifting the focus away from an inter-annual deviation from a base
306 period in the North Pacific onto the weather conditions experienced by individuals *in situ*,
307 and by delimiting the window of vulnerability to warm SST: the 1st to 5th weeks of
308 incubation.

309 SST could influence hatching success in two ways: by affecting food availability and
310 thence adult body condition, or by providing parents with a cue to upcoming food
311 availability for hatchlings and thereby affecting their investment decisions. According to
312 life-history theory, long-lived iteroparous species are expected to assign their finite supply
313 of resources in a way that allows them to evade or mitigate the impacts of stressful
314 environments on adult survival –the parameter with greatest impact on their lifetime fitness
315 (Gaillard and Yoccoz 2003; Boyce et al. 2006). Confronted with high SST during
316 incubation, blue-footed boobies may lower their current reproductive investment, as do
317 wood ducks (*Aix sponsa*; Hepp et al. 2005) and tree swallows

318 (*Tachycineta bicolor*; Pérez et al. 2008), for example, by defending clutches less vigorously
319 against seagulls or even abandoning them.

320 On the other hand, moderate maximum rainfall between the 2nd and 5th weeks of incubation
321 depressed hatching success. Rainfall can affect hatching success by dampening substrates
322 and decreasing egg temperatures and/or by exposing eggs to humid and cold air –via
323 increased conductance (Heenan 2013)–, possibly increasing exposure and proliferation of
324 pathogens on the shell, malformations and mortality of embryos (Godard et al. 2007; Noiva
325 et al. 2014). The increase in hatching success when maximum rainfall exceeded 4 mm was
326 unexpected and might be explained by an increase in parental attentiveness during heavy
327 rain (e.g. Fu et al. 2017). However, behavioural observations and nest temperature
328 monitoring are needed to support this idea.

329 Fledging success and fledgling body condition

330 During the last 4 weeks of brood care (7th-10th weeks), the occurrence of rainfall increased
331 the proportion of chicks that fledged while high minimum SSTs present during the 4th to 7th
332 weeks of rearing decreased the body condition of the offspring at fledging. Here again,
333 rainfall and SST may function as cues to future availability of food for fledglings and elicit
334 changes in parental investment increases when it rains and decreases when SSTs are high.
335 Summer rainfall increases chlorophyte abundance in coastal seas (Thompson et al. 2015)
336 because atmospheric nutrient input and river-delivered nutrients increase with rain (e.g.
337 Kim et al. 2014). This increase in ocean productivity leads, in turn, to an increase in the
338 abundance of the engraulids (i.e., anchovies) and clupeids (i.e., sardines and herrings) that
339 blue-footed boobies –most commonly– prey on. Rainfall at the end of brood care could
340 stimulate parents to increase food provisioning as their nestlings reach their maximum pre-
341 flight weight (at ages 65-70 and 60-65 days for females and males, respectively; Drummond

342 et al. 1991) at the expense of their own body condition (for example, Souther hemisphere
343 blue-footed boobies; Velando 2002)— a condition that they may quickly regain after their
344 offspring start to fly. Such a stimulation may help both survival expectations of nestlings
345 and overall fitness of breeding adults.

346 On the other hand, warm SSTs in the middle of the rearing period can signal a future food
347 shortage, a scenario under which parental investment is expected to decrease in preparation
348 for future reproduction (for example, common fiscals *Lanius collaris* (Cunningham et al.
349 2013); pied babbler *Turdoides bicolor* (Wiley and Ridley 2016); tree swallows (Tapper et
350 al. 2020)), resulting in lower provisioning rates or even the allocation of poor-quality food
351 to the young —that is, low-lipid food (González-Medina et al. 2018)—, which, ultimately,
352 leads to offspring with low body condition at fledging. Measures of body condition of both
353 adults and offspring at this stage are needed along with data on prey abundance, to further
354 explore this idea.

355 The positive effect of rainfall on fledging success is consistent with the previously reported
356 unfavourable effect of negative SOI values in December-March on the average fledging
357 success of these birds (Ancona et al. 2011). Negative SOI values may coincide with low
358 rainfall (e.g. in Australia, negative SOI values can correspond to below average rainfalls;
359 Stone and Auliciems 1992) and thus support the correlation between low fledgling success
360 and low levels of rainfall (this study). The exception to this pattern occurs during El Niño
361 events —whose strength can be characterized by how negative the SOI values are—, when
362 winter rainfalls occur, and are followed by a deficit of rain in summer in this part of Mexico
363 (Magaña et al. 2003). This pattern does not affect our overall interpretation since blue-
364 footed boobies tend to skip reproduction when strong El Niño events develop before and

365 during the breeding season, for example, the events of 1992 and 2016 where less than 30
366 breeding pairs tried to reproduce on the island (unpublished data).

367 Intra-annual weather variability

368 As expected, years with more variable mean SST values during each nests' 1st to 5th weeks
369 of incubation were more successful –and colder– than years with relatively constant SSTs.
370 Within-season variability in SST, which is negatively correlated with wind speed (Wang et
371 al. 1999), may facilitate the natural cycle of primary productivity (Chavez et al. 2011):
372 nutrients upwell when SSTs are cold and wind speeds are high, and then the organic matter
373 sinks and decays–later converting back into nutrients–when SSTs are warm and wind
374 speeds are low. We found weak and inconclusive evidence of lesser and greater hatching
375 and fledging success in years with more variable rainfall, respectively. The
376 inconclusiveness of these findings might be due to the outstanding range of rainfall CVs.
377 Within season rainfall variability may be due to the rains accompanying the end of the
378 hurricane season, which ends in November (CONANP 2005) and that followed by a dry
379 season in Spring (this study), and by the anomalous winter rainfalls present during El Niño
380 years, which are followed by summer droughts (Magaña et al. 2003). On the contrary, the
381 restrictive range of minimum SST CVs might explain the inconclusiveness of their negative
382 effect of on fledgling body condition. Blue-footed boobies may raise fledglings only when
383 minimum SSTs are relatively stable, but more morphologic and yearly data are needed to
384 confirm this.

385 Here we showed for a population of blue-footed boobies off the Pacific Coast of Mexico
386 that offspring survival and condition at independence varied in function of the weather
387 conditions experienced during the incubation and rearing periods. We proposed
388 mechanisms by which these long-lived birds may optimize their fitness when facing

389 variations in weather conditions after laying. In the context of climate variation in the
390 tropics, which is predicted to increase with climate change (Williams et al. 2007; Corlett
391 2012), our results may provide insight into how wild populations can respond to
392 unpredictable weather variations during their reproduction. Nevertheless, direct behavioural
393 observations are needed to evaluate these regulatory mechanisms along with analyses of the
394 potential future payoffs of reducing current reproductive investment. Future research
395 should focus on how these conditions affect surviving offspring's adult phenotype.
396 Ultimately, more research on how tropical species respond to variable weather conditions is
397 required to predict the impacts of climate change within the biodiversity hotspot that is the
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655

656 **Tables**

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

Parameter	Median	89% HPD
Intercept	-0.599	-0.991, -0.198
Mean SST	-1.001	-1.252 -0.768
Mean SST²	-0.720	-1.062, -0.395
Maximum rainfall	-0.719	-1.397, -0.053
Maximum rainfall²	1.091	0.469, 1.734
Clutch size*		
2	0.660	0.406, 0.932
3	0.474	0.164 0.791
Laying date	0.245	0.038, 0.441
Females' age	0.057	-0.117, 0.224
Females' age²	-0.473	-0.694 -0.249
Random effects	Std. Dev.	n
Male ID	0.89	1450
Female ID	0.60	1306
Lay date	0.71	907
Year	0.64	26

658 Terms whose highest posterior density (HPD) intervals did not contain zero are presented
 659 in boldface type. *Clutches of one egg were used as reference level.

660

661 Table 2. Effect of maximum rainfall on the proportion of chicks that fledged in 966 broods.

Parameter	Median	89% HPD
Intercept	0.505	0.136, 0.904
Brood size*		
	2	-0.692
	3	-1.243, -0.525
Maximum rainfall	0.834	0.459, 1.217
Hatching date	-0.645	-0.934, -0.367
Random effects	Std. Dev.	n
Male ID	0.480	756
Female ID	0.350	729
Hatch date	0.320	492
Year	0.950	26

662 Parameters whose highest posterior density (HPD) intervals did not contain zero are
 663 presented in boldface type. *Nests rearing only one chick were used as reference level.

664

665 Table 3. Effect of minimum SST on the body condition of 411 fledglings.

Parameter	Median	89% HPD
Intercept	-0.070	-0.108, -0.032
Brood size*		
	2 -0.038	-0.059, -0.016
	3 -0.080	-0.134, -0.025
Minimum SST	-0.183	-0.216, -0.152
Hatching date	0.005	-0.030, 0.039
Random effects	Std. Dev.	n
Male ID	0.030	365
Female ID	0.024	357
Nest ID	0.026	411
Hatch date	0.036	238
Year	0.087	21

666 Terms whose highest posterior density (HPD) intervals did not contain zero are presented
 667 in boldface type. *Nests rearing only one chick were used as reference level.

668

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

Parameter	Median	89% HPD	range of CVs
Hatching success (n = 26 years)			
Intercept	-0.220	-0.290, -0.154	-
Mean SST CV	0.846	0.678, 1.010	0.77% -9.29%
Minimum rainfall CV	-0.068	-0.255, 0.121	0%-486.81%
Fledging success (n = 26 years)			
Intercept	-0.103	-0.214, -0.000	-
Maximum rainfall CV	0.148	-0.080, 0.382	0%-306.46%
Fledgling body condition (n = 21 years)			
Intercept	-0.095	-0.141, -0.046	-
Minimum SST CV	-0.033	-0.131, 0.064	0%-5.61%

671 Left column shows the effect of the coefficient of variation of the yearly weather
 672 conditions' critical time windows. For every weather condition, the range of coefficient
 673 variation is reported in the right column. Parameters whose highest posterior density (HPD)
 674 intervals did not contain zero are presented in boldface type.

675

676 **Figure legends**

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

680 Figure 2. Weather conditions on Isla Isabel and its surrounding waters (1988-2019)

681

682 Figure 3. a) Critical time windows of SST and rainfall during the boobies' reproduction.

683 Effects of b) mean SST and c) minimum rainfall on hatching success, and effect of d)

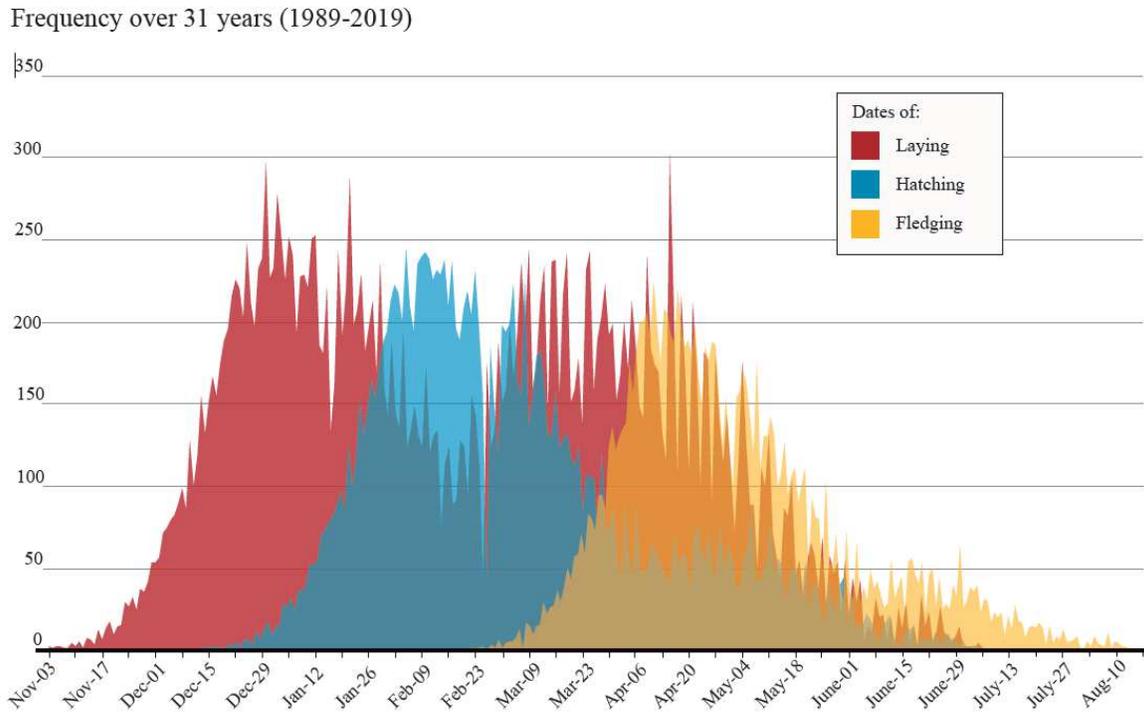
684 maximum rainfall on fledging success. Median effects of each weather condition and their

685 89% highest posterior density intervals are presented; dots are raw observations.

686

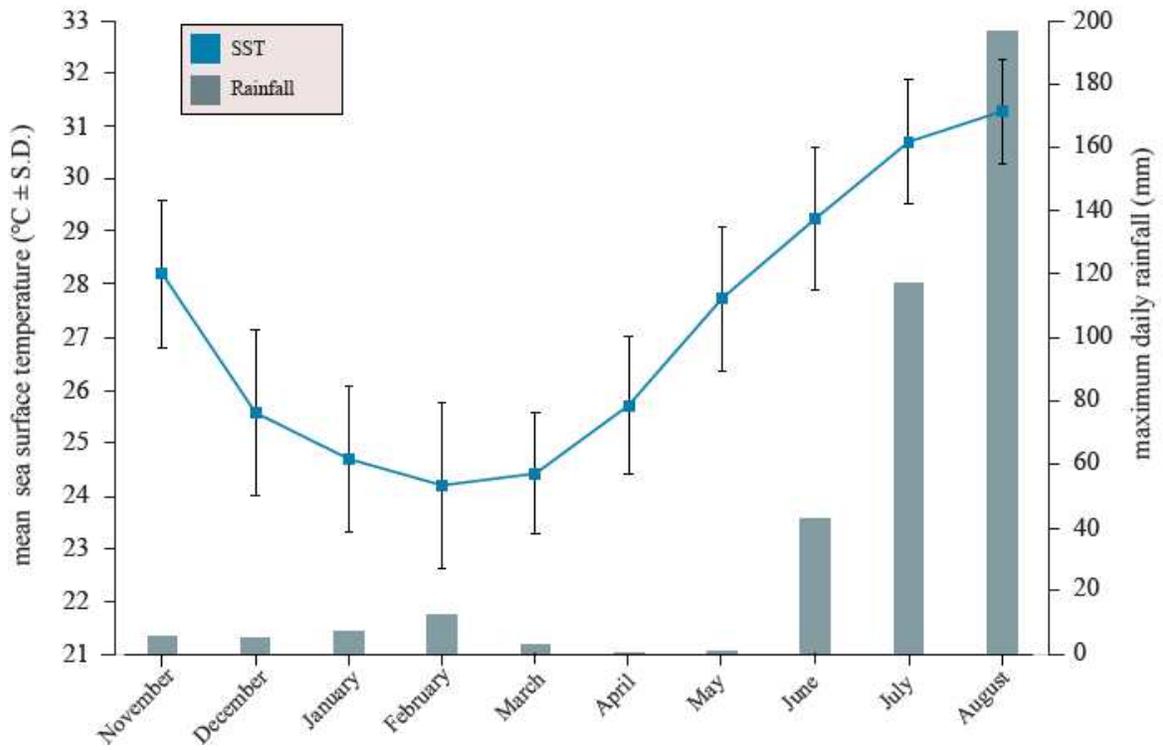
687 **Figures**

688 Figure 1.



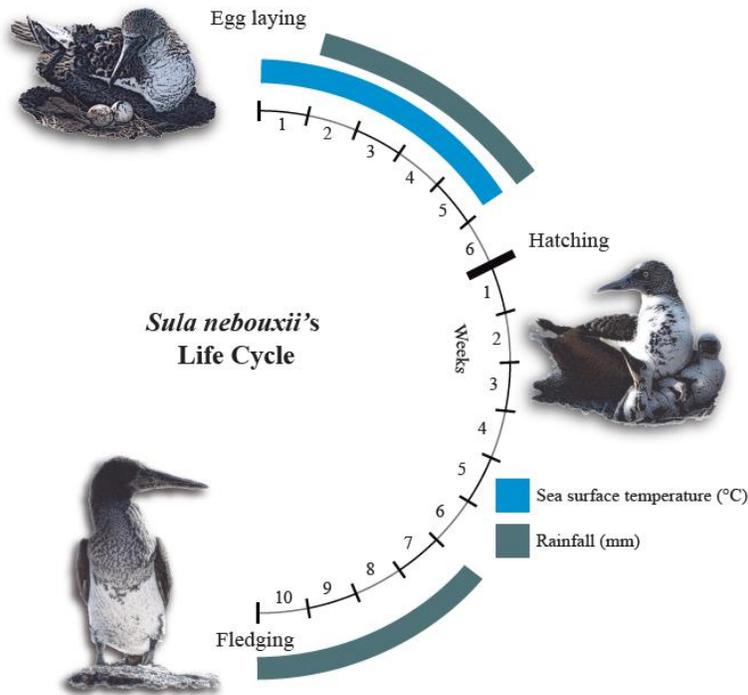
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690 Figure 2.

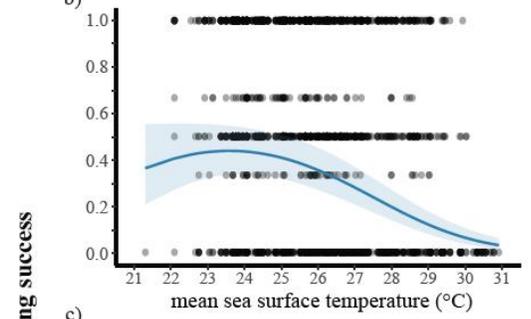


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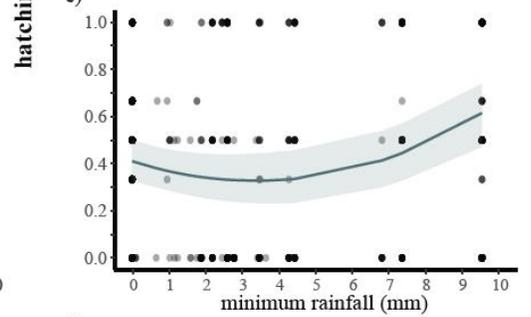
a)



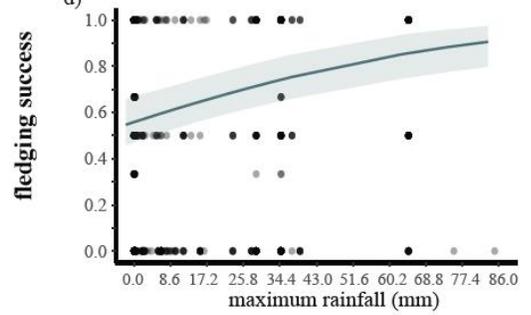
b)



c)



d)



Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Dataset.xlsx](#)