UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE ECOLOGÍA

PLASTICIDAD DE HISTORIA DE VIDA ANTE EL NIÑO: AJUSTES DE INVERSIÓN REPRODUCTIVA EN UN AVE DE VIDA LARGA

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

JOSÉ SANTIAGO ORTEGA RAMÍREZ

TUTOR PRINCIPAL DE TESIS:
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MÉXICO, CD. MX. ENERO, 2024.

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Presente

Me permito informar a usted, que el Comité Académico, del Posgrado en Ciencias Biológicas, en su reunión ordinaria del día **11 de septiembre del 2023,** aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del estudiante **ORTEGA RAMÍREZ JOSÉ SANTIAGO** con número de cuenta **309137630** con la tesis titulada: **"PLASTICIDAD DE HISTORIA DE VIDA ANTE EL NIÑO: AJUSTES DE INVERSIÓN REPRODUCTIVA EN UN AVE DE VIDA LARGA",** Bajo la dirección del **DR. HUGH MICHAEL DRUMMOND DUREY**, quedando integrado de la siguiente manera:

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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
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Índice

Resumen

El cambio climático antropogénico está causando cambios ambientales rápidos y persistentes, representando una amenaza significativa para la biota. En consecuencia, las poblaciones silvestres están utilizando diversas estrategias para hacer frente al ambiente en rápida transformación, como cambios en su rango geográfico, plasticidad fenotípica y adaptación local y rápida. La importancia de las respuestas plásticas en rasgos de historia de vida está aumentando en el contexto del cambio climático antropogénico en curso, pero la mayoría de los estudios se han centrado en especies templadas, lo que resalta la necesidad de más investigaciones sobre cómo las especies tropicales ajustan sus rasgos de historia de vida en respuesta a variaciones ambientales para predecir los impactos del cambio climático en los puntos calientes de biodiversidad que son los trópicos.

Esta tesis doctoral tuvo como objetivo estudiar los ajustes en la historia de vida de las hembras de bobos de patas azules (*Sula nebouxii*) en respuesta a los indicadores de la productividad primaria del océano (PPO), que proporcionan información sobre la disponibilidad de presas. Se analizaron nueve años de datos demográficos para determinar si las hembras muestran plasticidad en el tamaño de puesta en respuesta a las variables de la PPO y si esta plasticidad está bajo selección. Además, se evaluaron 32 años de datos demográficos para examinar los efectos de las condiciones meteorológicas durante diferentes etapas de la reproducción en el éxito de eclosión y emplumado, así como en la condición corporal de las crías al emplumar. También se investigó si en los años con condiciones ambientales más estables los bobos tuvieron menos éxito reproductivo que en años con mayor variabilidad.

Los resultados mostraron que las hembras de bobos de patas azules aumentaron el tamaño de sus puestas cuando aumentaron las concentraciones de clorofila-α en las aguas alrededor de Isla Isabel antes de la reproducción. Esta plasticidad en el esfuerzo reproductivo en respuesta al nivel de recursos fue consistente entre diferentes indicadores de la PPO. Además, se detectó una correlación negativa entre temperaturas altas del mar durante casi todo el periodo de incubación y el éxito de eclosión, mientras que la presencia de precipitación a la mitad de la etapa de incubación correlacionó positivamente con el éxito de emplumado. También se encontró una correlación negativa entre temperaturas cálidas del mar durante presentes durante casi todo el desarrollo temprano de la progenie y la condición corporal de las crías al emplumar. Con base en estos resultados, se propusieron dos mecanismos potenciales mediante los cuales las condiciones meteorológicas locales podrían influir en el éxito de eclosión y emplumado, así como en la condición corporal de los polluelos: (1) afectando la disponibilidad de alimento para los padres y su condición corporal, y (2) sirviendo como señal para ajustar la inversión parental en función de la disponibilidad futura de alimento para las crías. En conclusión, las hembras de los bobos de patas azules de la costa del Pacífico de México mostraron ajustes consistentes en su esfuerzo reproductivo en respuesta a los cambios ambientales, aparentemente optimizando su adecuación según la disponibilidad de presas a lo largo de la temporada de reproducción.

Palabras clave: plasticidad fenotípica, inversión reproductiva, ambiente cambiante, condiciones meteorológicas, aves marinas

Abstract

Anthropogenic climate change is causing rapid and persistent environmental changes, posing a significant threat to the biota. Consequently, wild populations are using various strategies to cope with the fast-changing environment, such as geographic range shifts, phenotypic plasticity, and local and rapid adaptation. The importance of plastic responses in life history traits is increasing in the context of ongoing anthropogenic climate change, but most studies have focused on temperate species, highlighting the need for further research on how tropical species adjust their life history traits in response to environmental variations to predict the impacts of climate change in the biodiversity hotspots that are the tropics. This doctoral thesis aimed to study the life history adjustments of female blue-footed boobies (*Sula nebouxii*) in response to ocean primary productivity indicators (PPIs), which provide information about prey availability. The study analysed nine years of demographic data to determine if females exhibit plasticity in clutch size in response to PPI variables and if this plasticity is under selection. Additionally, 32 years of demographic data were evaluated to examine the effects of changing weather conditions during different stages of reproduction on hatching and fledging success, as well as the body condition of chicks when fledging. The study also investigated if years with more stable environmental conditions had less reproductive success than those with higher variability.

Results showed that female blue-footed boobies increased their clutch size when chlorophyll-α concentrations increased in the waters around Isla Isabel increased before reproduction. This plasticity in reproductive effort in response to changing resources was consistent across different PPI indicators. In addition, a negative correlation was detected between high sea temperatures during almost the entire incubation period and hatching success, while the presence of precipitation in the middle of the incubation stage positively correlated with fledging success. A negative correlation was also found between warm sea temperatures during most of the progeny's early development and the chicks fledging body condition at fledging. Based on these results, two potential mechanisms were proposed to explain how local weather conditions could influence hatching and fledging success, and the condition of chicks: by affecting food availability for parents and their body condition, and by serving as a signal to adjust parental investment based on future food availability for offspring. In conclusion, female blue-footed boobies from the Pacific coast of Mexico displayed consistent adjustments in their reproductive effort in response to environmental changes, seemingly optimizing their fitness based on prey availability throughout the breeding season.

Keywords: phenotypic plasticity, reproductive investment, shifting environment, weather conditions, seabirds

Introducción general

El cambio climático antrópico está causando cambios ambientales rápidos y persistentes, lo que representa una amenaza significativa para la biota terrestre. Además del preocupante aumento de las temperaturas globales, ya que diversos modelos climáticos predicen un incremento en la variabilidad de las condiciones climáticas, especialmente en regiones (sub)tropicales (Bathiany et al., 2018). A la par, se esperan eventos climáticos extremos más frecuentes e intensos (Corlett, 2012; Kusunoki et al., 2020; Stott, 2016; Thornton et al., 2014). Para hacer frente a los desafíos de un ambiente rápidamente cambiante, las poblaciones silvestres pueden responder de diversas formas: desplazando su intervalo geográfico, exhibiendo plasticidad fenotípica y/o someterse a una adaptación local y rápida, e inclusive extinguiéndose localmente (Charmantier et al., 2008a; Chen et al., 2018; Tingley et al., 2012). Sin embargo, existen limitaciones como la filopatría, la fragmentación y la pérdida de hábitat, que pueden restringir las opciones de supervivencia de las poblaciones dentro de su área de distribución (Loarie et al., 2009). Además, la tasa de cambio ambiental puede superar la capacidad de adaptación local, especialmente si las poblaciones carecen de la variación genética necesaria para que actúe la selección natural, lo que pone en peligro su persistencia a largo plazo (Gomulkiewicz & Holt, 1995; Kopp & Matuszewski, 2014).

La plasticidad fenotípica –la capacidad de un genotipo de alterar su fenotipo en respuesta a las condiciones ambientales (Stearns, 1989)– ha sido postulada como un mecanismo crucial mediante el cual las poblaciones silvestres pueden responder a cambios ambientales rápidos, permitiéndoles persistir mientras ocurre la adaptación evolutiva (Chevin et al., 2010; Fox et al., 2019; Gienapp et al., 2008; Merilä & Hendry, 2014). Es importante notar que la plasticidad fenotípica es ubicua en todos los organismos (Acasuso-Rivero, Murren, Schlichting, & Steiner, 2019) y surge en respuesta tanto a factores externos, por ejemplo, patrones de cambio ambiental percibido por los individuos, como a factores internos de los organismos, por ejemplo, limitaciones del desarrollo o estado fisiológico dependiente de la edad.

La plasticidad fenotípica puede ser adaptativa o no adaptativa, e implicar ajustes repetidos en rasgos lábiles como la conducta (por ejemplo, fenología), fisiología (por ejemplo, límites térmicos) y rasgos de historias de vida (por ejemplo, esfuerzo reproductivo, supervivencia), e incluso cambios irreversibles en rasgos no lábiles, como la morfología (Crispo, 2007). En términos generales, se considera que la plasticidad es adaptativa cuando permite a los organismos mantener su adecuación en diferentes condiciones ambientales, es decir, cuando el genotipo de los organismos tenga una adecuación promedio superior a través de todos los ambientes en comparación con genotipos inflexibles. Es importante destacar que este tipo de plasticidad solo puede surgir y mantenerse 1) bajo condiciones ambientales heterogéneas, 2) cuando las señales ambientales (por ejemplo, condiciones meteorológicas o presencia de depredadores) son confiables, es decir, cuando la señal predice la presión selectiva que actuará sobre el rasgo plástico (ver Bonamour et al. 2019 para un resumen sobre la evolución de estas señales), y 3) cuando el costo de expresar plasticidad es relativamente bajo (Scheiner, 2013). Mientras tanto, la plasticidad no adaptativa puede ser mal adaptativa, por ejemplo, cuando el cambio en un rasgo perjudica la supervivencia de los organismos, o neutral, cuando las condiciones ambientales imponen restricciones fisiológicas que limitan o alteran la expresión de un rasgo (Gotthard & Nylin, 1995), produciendo fenotipos que exhiben una adecuación promedio reducida.

Al ser adaptativa, la plasticidad fenotípica permite que ocurra la acomodación genética y, por tanto, la adaptación local de la población (Crispo, 2007; Ghalambor et al., 2007a). Los dos mecanismos de acomodación genética más conocidos, cuyas definiciones varían dependiendo del autor, son el efecto Baldwin y la asimilación genética (Scheiner 2014, provee un panorama general de la caracterización errónea de estos términos). En general, ambos mecanismos se refieren al proceso mediante el cual la variación fenotípica no heredable se vuelve heredable a través de la selección natural (Ghalambor et al., 2007a). La diferencia entre ambos mecanismos radica en el efecto de la selección sobre la plasticidad. En el caso del efecto Baldwin, se espera que después de la expresión de plasticidad adaptativa, la selección mantenga o aumente los niveles de plasticidad en el rasgo focal. Por otro lado, la asimilación genética predice que, después de la expresión de plasticidad adaptativa, la selección limitará la expresión de plasticidad en el nuevo fenotipo, para que éste se exprese independientemente de las condiciones ambientales, es decir, se canaliza el fenotipo (Crispo, 2007; Ghalambor et al., 2007a).

Los costos asociados a la producción de un fenotipo plástico y el tipo de ambiente al que se enfrentan los organismos –el cual debe ser contextualizado en relación con la longevidad de los organismos (Kokko & Sutherland, 2001)– determinarán el tipo de adaptación genética que se favorezca (Crispo, 2007; Scheiner, 1993). Los costos asociados a la expresión de plasticidad pueden incluir, por ejemplo, el mantenimiento de los mecanismos sensoriales que inducen la respuesta plástica (como la glándula pineal), los costos asociados con la adquisición de información necesaria para detectar los cambios ambientales (como un mayor riesgo de depredación al moverse entre diferentes áreas en busca de alimento) o los costos genéticos, donde los genes que permiten la expresión de la plasticidad pueden interactuar de manera antagonista con otros genes y reducir la adaptabilidad (Dewitt, 1998). Si la plasticidad no es costosa y los organismos se enfrentan a ambientes fluctuantes, pero relativamente predecibles (Hidalgo Aranzamendi et al., 2019), se espera que se favorezca el efecto Baldwin, ya que este permite a los organismos mantener la plasticidad necesaria para sobrevivir en diferentes ambientes. Por otro lado, al enfrentarse a un ambiente que caiga fuera del rango de condiciones experimentadas por las poblaciones (por ej., un evento climático extremo), se favorecerá la asimilación genética al canalizar los procesos fisiológicos y de desarrollo mínimos necesarios para incrementar la probabilidad de persistencia en el nuevo ambiente (Ghalambor et al., 2007b; Reed et al., 2010). Es importante destacar que los procesos de canalización pueden llevar a la acumulación de variación fenotípicamente críptica, lo que significa que los fenotipos canalizados pueden mostrar cierta variación genética en determinadas condiciones ambientales o genéticas (Flatt, 2005).

Las historias de vida y su relación con la variabilidad ambiental.

Se sabe que las condiciones ambientales, tanto en sus efectos directos como indirectos, pueden influir en las estrategias de historia de vida de los organismos, es decir, en cómo éstos distribuyen sus recursos finitos entre supervivencia, crecimiento, y reproducción (Stearns, 1992). Estas estrategias de asignación de recursos se encuentran en un continuo que va desde las historias de vida rápidas, donde la reproducción tiene prioridad sobre la supervivencia, hasta las historias de vida lentas, donde ocurre lo contrario (Gaillard et al., 2005; Galipaud & Kokko, 2020; Sæther et al., 2013). En general, se espera que los organismos con historias de vida rápidas maduren temprano, tengan tamaños corporales pequeños, produzcan más descendencia en cada evento reproductivo, tengan una vida corta, un tiempo generacional corto, y tiendan a ser semélparos, es decir, se reproducen solo una vez (Roff, 1993). Por otro lado, se espera que los organismos con historias de vida lentas maduren más tarde, tengan una descendencia reducida en cada evento reproductivo, tengan una vida larga, tiempos generacionales largos, y tiendan a la iteropariedad, es decir, se reproducen múltiples veces (Boyce et al. 2006; Gaillard and Yoccoz 2003).

La posición de los organismos en el continuo rápido-lento puede predecir la plasticidad de sus rasgos de historia de vida. Se espera que los organismos con estrategias de vida lenta, al enfrentarse a numerosas condiciones ambientales a lo largo de su vida, exhiban un mayor nivel de plasticidad en rasgos de historia de vida, especialmente en el esfuerzo reproductivo (Ratikainen & Kokko, 2019). En condiciones favorables, estos organismos invertirán en reproducción en detrimento de su mantenimiento y supervivencia, mientras que en condiciones subóptimas o adversas disminuirán su inversión reproductiva a favor de la supervivencia (Ghalambor & Martin, 2001). Por lo tanto, no es sorprendente que la mayoría de los estudios sobre plasticidad en rasgos de historia de vida se centren en especies con historias de vida lentas (por ej. Keogan et al., 2018; Nussey et al., 2007). En cambio, para los organismos con historias de vida rápidas, lo óptimo sería expresar poca o nula plasticidad en rasgos de historia de vida, ya que cualquier desajuste entre el fenotipo y el ambiente puede ser costoso en términos de adecuación (Kokko & Sutherland, 2001). Por lo tanto, se favorecería la expresión rígida del fenotipo independientemente del ambiente al que se enfrenten, es decir, un fenotipo canalizado. Sin embargo, en estos organismos, es más probable observar plasticidad en rasgos no lábiles, como la morfología, en respuesta a las fluctuaciones ambientales, lo que a su vez puede desencadenar cambios en otros rasgos de historia de vida (por ej. Reznick, Bryga, and Endler 1990).

Plasticidad fenotípica en aves

La variabilidad climática y su impacto en las especies de aves han sido objeto de numerosos estudios. Se sabe que las condiciones ambientales en las zonas de reproducción influencian fuertemente el éxito reproductivo y la inversión reproductiva de las aves (Forchhammer et al., 1998). El tiempo –*sensu* condiciones meteorológicas– puede afectar directamente la reproducción de las aves, por ejemplo, a través de inundaciones de nidos causadas por la lluvia (Simeone et al., 2002), o indirectamente, al alterar la disponibilidad de alimento (Shutt et al., 2019). Ante estos retos, las aves pueden ajustar su fenotipo, por ejemplo, modificando el momento de su reproducción para evitar condiciones desfavorables y sincronizarse con la disponibilidad de alimentos (Charmantier & Gienapp, 2014; Glądalski et al., 2018). Innegablemente, en el contexto del cambio climático antrópico en curso, las respuestas plásticas en rasgos fenológicos están adquiriendo cada vez más importancia Empero, es importante mencionar, que la mayoría de los estudios se han centrado principalmente en cómo los cambios en las temperaturas invernales y primaverales afectan la expresión de plasticidad fenológica en especies templadas (Dunn, 2019; Parmesan & Yohe, 2003). Consecuentemente, más investigación sobre cómo las especies tropicales ajustan éste y otros rasgos de historia de vida en respuesta a variaciones en las condiciones ambientales será esencial para evaluar los impactos del cambio climático dentro del punto crítico de biodiversidad que son los trópicos.

Es importante destacar que los organismos deben tomar múltiples decisiones a lo largo de las diferentes etapas de reproducción, por ejemplo, durante la incubación y la crianza. Por lo tanto, además de los desplazamientos fenológicos, es posible que los organismos deban ajustar sus estrategias reproductivas en respuesta a los cambios ambientales que ocurren una vez que han iniciado su reproducción. Aunque algunos estudios han examinado cómo las condiciones meteorológicas promedio presentes durante la temporada reproductiva afectan la reproducción de las aves, todavía no se ha investigado adecuadamente la influencia de la variabilidad ambiental durante toda la temporada reproductiva sobre el éxito reproductivo. Por lo que existe un interés creciente en estudiar cómo la variabilidad ambiental durante las etapas de incubación y cuidado de las crías afecta las decisiones de reproducción de los progenitores, así como el desarrollo y la supervivencia de las crías (Bordjan y Tome, 2014; Rodríguez y Barba, 2016).

Dado que la variabilidad meteorológica puede alterar la demografía de las poblaciones, especialmente en especies con períodos de crianza prolongados como las aves marinas (Lescroël et al., 2016), comprender cómo responden los organismos a esta variabilidad intra-anual resulta crucial. En especies con historias de vida lentas, la capacidad de mostrar plasticidad en el esfuerzo reproductivo en respuesta al ambiente puede ser fundamental para su supervivencia a largo plazo (Ghalambor & Martin, 2001; Ratikainen & Kokko, 2019). Sin embargo, todavía se sabe poco acerca de la naturaleza adaptativa y el impacto general de la plasticidad fenotípica en el esfuerzo reproductivo a lo largo de la trayectoria de vida de un organismo. Este conocimiento puede contribuir a los esfuerzos de conservación y al desarrollo de estrategias efectivas para mitigar los efectos del cambio climático en las poblaciones de aves.

El bobo de patas azules como modelo de estudio

Las aves marinas, conocidas por su larga esperanza de vida y su fidelidad a los sitios de reproducción (Anderson & Apanius, 2003; Danckwerts et al., 2021a; Kim et al., 2007), ofrecen una excelente oportunidad para estudiar la plasticidad de la historia de vida en respuesta al cambio ambiental, especialmente en relación con las variaciones en la productividad primaria del océano (PPO), que influyen fuertemente en su éxito reproductivo (Ainley et al., 1995; Sydeman et al., 2006). Estas aves, que generalmente tienen historias de vida lentas y se encuentran en un estatus de alta vulnerabilidad ante las actividades humanas (BirdLife International, 2022) pueden depender de la plasticidad de su historia de vida para su persistencia y aptitud a largo plazo, ya que su adaptación a nuevos entornos tiende a ser lenta (Sydeman et al., 2015).

En esta tesis, usé a las hembras del bobo de patas azules *Sula nebouxii* de la Isla Isabel, México (21°50'59.0"N 105°52'54.0"W), como modelo de estudio. El bobo de patas azules es un ave de historia de vida lenta que se alimenta principalmente de peces pelágicos (Ancona et al., 2012; González-Medina et al., 2018). Los bobos pueden iniciar su reproducción entre su primer y doceavo año de vida (Drummond et al., 2011), y llegar a vivir hasta 25 años de edad (Ortega et al., 2017), aunque tienen una vida reproductiva mediana de 9 años (Ortega et al., datos sin publicar). Después de un periodo de cortejo, que puede durar entre 1 a 9 semanas (Stamps et al., 2002), las hembras ponen de 1 a 3 huevos. El cuidado parental es compartido por ambos padres desde la incubación, que dura ~41 días, hasta el emplumado de las crías a los 90 días de edad. Las hembras son ~25% a 32% más pesadas que los machos (Castillo & Chávez-Peón, 1983; Guerra & Drummond, 1995), y proveen de dos a cinco veces más alimento a las crías (Guerra & Drummond, 1995).

En Isla Isabel, los bobos de patas azules se reproducen a lo largo de las estaciones boreales, desde principios de noviembre hasta mediados de agosto, lo que la expone a condiciones ambientales variables dentro y entre temporadas de reproducción (Ortega et al., 2021, 2022). Es conocido que a medida que la PPO disminuye alrededor del sitio de anidación (denotado por aumento de la temperatura superficial del mar) las presas más comunes del bobo son menos abundantes y se desplazan hacia el norte (Lluch-Cota et al., 2017; Morales-Bojórquez et al., 2003). Entonces, para mantener su adecuación ante la fluctuación en disponibilidad de alimento, se espera que los bobos ajusten su inversión reproductiva en función de los valores de PPO experimentados a través de las diferentes etapas de reproducción como serían el cortejo, incubación y cuidado de las crías. En particular, se esperaría que al enfrentarse a valores de PPO bajos, que denotan la baja disponibilidad de alimento para sus presas, o valores extremadamente altos de PPO, lo que indica la presencia de floraciones algales, las hembras de bobos de patas azules reduzcan su tamaño de puesta y cuidado parental, resultando en un menor éxito reproductivo anual, de esa manera evitando aumentar la probabilidad anual de mortalidad de las progenitoras.

En esta investigación, evalué si las hembras del bobo de patas azules 1) exhiben plasticidad en el tamaño de puesta en respuesta a cuatro indicadores de productividad primaria oceánica (fungiendo como sucedáneos de disponibilidad de presas), 2) si la selección está actuando sobre la plasticidad en tamaño de puesta, 3) si las condiciones meteorológicas posteriores al inicio de la reproducción afectan la inversión parental (medida como su éxito de eclosión y emplumado, y la condición corporal de las crías al momento de emplumar), y 4) si en los años con condiciones meteorológicas menos variables, que pueden llevar a eventos climáticos extremos (por ejemplo, sequías, inundaciones y olas de calor; Francis & Vavrus, 2012) eclosionan menos huevos, empluman menos crías y se crían emplumados con una menor condición corporal que los años más variables.

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Capítulo 1.

Clutch size adjustments in a neotropical seabird: a test of life history plasticity.

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Abstract

Rapid and sustained environmental changes pose significant challenges to wild populations. Phenotypic plasticity, the ability to alter the phenotype in response to environmental conditions, enables populations to cope with such changes. While phenological plasticity is well documented, plasticity in life history traits, such as reproductive effort, in response to environmental changes, remains poorly understood, especially in species with slow life histories. Using nine years of demographic data, we analysed the overall impact of plasticity in clutch size in response to proxies of food availability on the life history trajectory of the Blue-footed booby (*Sula nebouxii*) in Mexico. Our analyses revealed a population-wide adjustment of clutch size in response to ocean primary productivity. Specifically, females increased their clutch sizes in response to higher prey availability assessed from the concentrations of chlorophyll-α and particulate organic carbon in surface waters prior to the onset of reproduction. Importantly, we found no evidence for individual variation in plasticity of clutch sizes in response to these proxies of prey availability. Furthermore, our findings indicate that variation among females in clutch size did not substantially affect their life history trajectories: females with above-median clutch sizes did not produce more fledglings each year or exhibit higher annual mortality. Overall, our results suggest that female boobies exhibit plasticity in clutch sizes in response to prey availability prior to egg laying and that this response is consistent across individuals. Understanding the mechanisms underlying such responses is crucial for predicting the resilience of wild populations facing progressive environmental changes.

Keywords: Phenotypic plasticity; reproductive effort; clutch size; environmental changes; seabird; life history

Introduction

Currently, the Earth's biota is experiencing rapid and persistent environmental changes due to anthropic climate change. In the face of these challenges, wild populations may face extinction (Davis et al., 2005). Alternatively, they may persist by shifting their geographic range (e.g., Tingley et al., 2012), expressing phenotypic plasticity (e.g., Charmantier, McCleery, Cole, Perrins, Kruuk, Sheldon, et al., 2008) and/or undergoing rapid and local adaptation (e.g., Chen et al., 2018). However, certain populations may be constrained within their distribution range due to philopatry, habitat loss and fragmentation (Loarie et al., 2009). Furthermore, the pace of ongoing environmental change may exceed the capacity of local adaptation, especially if populations lack the necessary genetic variation for natural selection to act upon, thus jeopardizing their long-term persistence (Gomulkiewicz & Holt, 1995; Kopp & Matuszewski, 2014). Consequently, phenotypic plasticity – the ability of a single genotype to alter its phenotype in response to environmental conditions (Bradshaw, 1965; Stearns, 1989)– has been proposed as the primary mechanism by which wild populations can respond to rapidly changing environments (Gienapp et al., 2008; Merilä & Hendry, 2014), allowing them to persist while evolutionary adaptation occurs (Chevin et al., 2010; Fox et al., 2019).

One well-known example of phenotypic plasticity in response to environmental changes is phenological shifts, which involve changes in the timing of life-cycle events such as flowering or breeding (Donnelly et al., 2012). These behavioral adjustments can enable organisms to synchronize their reproductive activities with environmental conditions, such as food availability (Bonamour et al., 2020; Charmantier et al., 2008; Visser, 2013). Such adjustments can have long-term implications for the persistence and fitness of populations. It is important to note that not all plastic responses are adaptive; some may be neutral when environmental constraints limit or alter trait expression but do not affect fitness, or even maladaptive if trait changes hinder an organism's survival (Gotthard & Nylin, 1995). In the context of current anthropic climate change, plastic responses in phenological traits are becoming increasingly important as environmental conditions continue to shift (Zettlemoyer & Lau, 2021).

In addition to phenological shifts, species may need to adjust their life history trajectories to cope with rapid environmental changes. According to life-history theory, adjustments in life history traits, which involve trade-offs between survival and reproduction, are expected to occur in response to environmental conditions (Stearns, 1989). For instance, species at the slower end of the fast-slow life continuum, characterized by iteroparity, low reproductive rates, slow developing offspring, long lifespans and high trophic levels (Gaillard et al., 1989), are likely to exhibit plasticity in reproductive effort (Ghalambor & Martin, 2001; Ratikainen & Kokko, 2019). By modifying their reproductive effort to take advantage of favourable environments or to mitigate the impacts of stressful environments on adult survival (the parameter with the utmost impact on their fitness; Boyce et al., 2006; Gaillard et al., 2003), these species can maintain their fitness across different environmental conditions. However, while plasticity in life history traits is widely recognized as a common phenomenon (Acasuso-Rivero et al., 2019), little is known about whether phenotypic plasticity in reproductive effort in response to environmental cues is under selection or how it alters the overall life history trajectory of an organism.

Seabirds, known for their relatively long lifespans and strong breeding site fidelity (Anderson & Apanius, 2003; Danckwerts et al., 2021; Sin Yeon Kim et al., 2007), provide an excellent opportunity to study life history plasticity in response to environmental change, particularly in relation to variations in ocean primary productivity – a proxy of prey availability that strongly influences their breeding success (Ainley et al., 1995; Sydeman et al., 2006). These birds, which generally have slow life histories and are highly vulnerable to anthropic threats (BirdLife International, 2022), may rely on life history plasticity for their long-term persistence and fitness, as their adaptation to new environments tends to be slow (Sydeman et al., 2015).

In this study, we assessed whether females of the blue-footed booby *Sula nebouxii*, a long-lived neotropical seabird that feeds primarily on pelagic fishes (Ancona et al., 2012; González-Medina et al., 2018), adjust their clutch sizes in response to four proxies of primary ocean productivity. Our study population reproduces throughout the boreal seasons (i.e., those pertaining to the Northern Hemisphere) from early-November to mid-August, exposing it to varying environmental conditions within and between breeding seasons (Ortega et al., 2021, 2022). Over a 30-year period, local weather and demographic data from this colony revealed a strong correlation between local weather conditions and breeding success (Ortega et al., 2022). Specifically, warm sea surface temperatures (SST), which are known to affect the distribution and abundance of pelagic fishes, which feed on phytoplankton (Lluch-Cota et al., 2017; Morales-Bojórquez et al., 2003), were associated with a reduction in hatching success, implying a decrease in breeding investment during incubation (Ortega et al., 2022). Similarly, decreased rainfall, which is linked to atmospheric nutrient input and river-delivered nutrients in coastal seas (Kim et al., 2014; Thompson et al., 2015), was associated with a decline in fledging success (Ortega et al., 2022).

However, the relationship between weather conditions, such as SST, and primary productivity is complex (e.g., Feng et al., 2022; Trenggono et al., 2018). We anticipate that female boobies will exhibit greater sensitivity to closer proxies of both ocean primary productivity and prey abundance (e.g., Feyrer et al., 2017), such as concentration of chlorophyll- α (Chl-α) and particulate carbon particles (POC), or water turbidity (KD490) than to SST. We therefore expect a reduction in clutch sizes when our four proxies of primary productivity, including SST, exhibit very low values, indicating limited prey availability due to a scarcity of phytoplankton, or extremely high values, indicating the presence of algal blooms. Additionally, we predict that more plastic females, that is, those that have a higher variation in their clutch sizes across their breeding events in response to these proxies would have higher annual fledgling production and a greater annual probability of survival than less plastic females.

Methods

Study population

Blue-footed boobies of Isla Isabel, Nayarit, Mexico (21°50’59.0”N 105°52’54.0”W) first reproduce between their first and twelfth year of life, with recruitment after 12 years being unlikely (Drummond et al., 2011). They can live up to 25 years (Ortega et al., 2017), but recruits have a median reproductive lifespan of 9 years (Ortega et al. unpublished data). After a courtship period that may last ~1-9 weeks (Stamps et al., 2002), females typically lay 1-3 eggs. Parental duties are shared by both parents from incubation, which lasts ~41 days, through chick fledging at ~90 days from hatching. Females are ~25% to 32% heavier than males (Castillo & Chavez-Peón, 1983; Guerra & Drummond, 1995), and provide two to five times more food to their offspring (Guerra & Drummond, 1995). Among 33,975 nests established between 1989 and 2022 in the study population, two-egg clutches were the most common (59%), followed by one-egg clutches (30%), and three-egg clutches (~10%) (Ortega et al. unpublished data). Nests with more than three eggs are rare, representing fewer than ~0.01% of all nests.

Demographic data

Individual blue-footed boobies in two study areas of the Isla Isabel colony were identified by alphanumeric steel bands fitted at age 70 days. Throughout each field season (roughly February through July), the nest contents of breeding pairs were recorded every 3 days until fledging (details in Drummond et al., 2003). This monitoring protocol enabled measurement of clutch sizes and estimation of egg laying dates (within a two-day error margin) while minimizing disturbance of incubating birds. Eggs were not manipulated or marked during monitoring, to avoid nest desertion.

Female and male recruits born between 1989 and 2020 had a median of 3 reproductive events, ~28% of them having only one (Ortega et al., unpublished data). From 1989 to 2022, 57% of breeding pairs established their clutches prior to the start of our field season, with the earliest estimated laying in early November. As egg disappearances were rare at the beginning of the field season, sizes of clutches established prior to the start of monitoring were assumed to be the number of eggs and nestlings present at the first inspection. This assumption was possible because Hermann's gulls *Larus heermanni*, the only egg predators, arrive on the island around February (CONANP, 2005) and milk snakes *Lampropeltis polyzona*, the only chick predators, are seldom active in the booby colony during winter (Ortega et al., 2021). Egg predation by gulls can occur opportunistically, with individual gulls seizing eggs from unattended or poorly defended nests, or through coordinated group attacks, where a few gulls induce an incubating parent to rise up and one of them seizes an egg (Ortega et al, personal observations). Laying dates of nestlings present at the start of monitoring were estimated by subtracting their age –estimated from beak and ulna growth curves– plus the mean incubation period of a booby egg from the date when monitoring began (Drummond and Rodríguez, unpublished data).

Ethical note

Permission for fieldwork was given by Mexican authorities (SEMAR, CONANP, SEMARNAT and Parque Nacional Isla Isabel). We followed the ASAB /ABS (2023) Guidelines for the treatment of animals. During our annual monitoring, two monitors visually inspected nests and parents without handling them. To reveal nest contents and to read caretaking birds´ steel rings, the monitor carefully nudged the adult backward with a forked stick. After withdrawing from the nest, the monitors waited nearby until eggs and young chicks were covered by a parent and, if the parent flew from its nest, covered the eggs with leaves to prevent predation by overflying gulls.

Proxies of ocean primary productivity

To assess ocean primary productivity, we utilized satellite remote sensing data on the ocean's colour and on the interaction between light and the water column. Specifically, we employed data on the following proxies: 1) chlorophyll-α concentration ([Chl-α]), which indicates the presence of photosynthetic pigment found in phytoplankton and some algae; 2) particulate carbon particle concentration ([POC]), representing photosynthesis by-products and other organic matter, including zooplankton; 3) diffuse attenuation coefficient at a wavelength of 490 nm (KD490), a measure of water turbidity that indirectly reflects the concentration of particles that absorb or scatter light, such as Chl-α and dissolved organic matter; and 4) night-time sea surface temperatures (SST).

Satellite remote sensing data

For the period 2012-2022, we obtained daily mean values of Chl-α, POC, KD490, and SST within the species' average foraging range (~30 km; Weimerskirch et al., 2009; Zavalaga et al., 2008). The daily values of all grids within the foraging area of the species (~30 km in each cardinal direction from the island's centre) were averaged for each of the primary productivity indicators obtained. These grids had a spatial resolution of 4 km, resulting in a coverage area of approximately 60 × 52 km. Chl-α, POC, and KD490 were measured by the Visible Infrared Imaging/Radiometer Suite abord the Suomi National Polar-orbiting Partnership satellite (VIIRS/S-NPP; NASA et al 2022a, 2022b, 2022c). SST values were derived from the Advanced Very High-Resolution Radiometer Pathfinder instruments aboard the NOAA's polar-orbiting satellites (v.5.3; Casey et al., 2010; Saha et al., 2018; available at https://www.ncei.noaa.gov/products/avhrr-pathfinder-sst). Night-time SST fields were used to mitigate the influence of irregular solar heating (c.f., Chin et al., 2017; Mauzole et al., 2020; Tomasetti et al., 2023).

Statistical analyses

All analyses were conducted using the R statistical environment (R Development Core Team, 2022). For all generalized linear mixed models, continuous fixed variables were standardized before model fitting to enhance the interpretability of parameter estimates (Cade, 2015; Grueber et al., 2011). The error distributions for the GLMMS explaining the long-term fluctuations of the environmental conditions encircling Isla Isabel were assumed to be Gaussian with an identity link function, while the models explaining clutch size were presumed to be Poisson with a log-link function. Weakly informative priors were included in all Bayesian models to stabilize computation, prevent overfitting, and avoid erroneous estimations of large effect sizes (Gelman et al., 2008; Lemoine et al., 2016). A normal prior of N(0,1) was assigned to the fixed effects, implying that the majority of responses were expected to fall within one standard deviation of the median response value, and that large effects should be unusual (Lemoine et al., 2016). The posterior distribution of the parameters, along with their 89% highest posterior density intervals (HPD), which represent high-probability interval of parameter values (McElreath, 2020), were drawn by running four randomly initiated Markov chains. Each Markov chain ran for 10,000 iterations with a burn-in of 1000 iterations. Posterior predictive checks were performed for each generalized linear mixed models (GLMMs) using the *launch_shinystan* function of the *shinystan* package (Gabry, Veen, et al., 2022). Variable standardization was conducted using the *rescale* function of the package *arm* (Gelman et al., 2016) Bayesian GLMMs were built using the *stan_glmer* function in the *stanarm* package (Gabry, Ali, et al., 2022).

Environmental conditions around Isla Isabel

To analyse the decade-long fluctuations spanning from 2012 to 2022 in [Chl-α], [POC], KD490, and SST in the waters surrounding Isla Isabel, we computed average values for each environmental parameter across season periods (namely, Autumn, Winter, Spring, and Summer). For every environmental condition a GLMM was fitted. These models incorporated both linear and quadratic terms of time (expressed in years as a continuous variable), and season (a four-level categorical variable) as fixed variables. The inclusion of the quadratic term in the time component allowed us to account for potential oscillations arising from large scale ocean-atmospheric phenomena, such as El Niño-Southern Oscillation (ENSO). All models included year as a random effect to account for pseudoreplication and potential confounding effects.

Clutch size adjustments

The sample included 1203 female breeders and 1316 male breeders of known age (i.e., banded as fledglings) that recruited between their 1st and 12th years of life. The clutch sizes of these females were tallied across 9 breeding events from 2013 to 2022. Our sample omits nests established in 2016, a year marked by an exceptional El Niño event (Santoso et al., 2017). During this particular year, a mere 34 nests were established, and due to the incompleteness of their reproductive records, these nests were not considered eligible for inclusion in our analysis. From 2013 to 2022, females had a median of 2 breeding events, while males had a median of 1 breeding event; the number of breeding events of both sexes ranged from 1 to 9 events. Approximately, 48% of female and 51% of male breeders reproduced only once in the 9 years of monitoring. The median age for both sexes was 9 years, with females ranging from 2 to 22 years and males from 3 to 23 years. Approximately 26% of clutches were established prior to the start of monitoring.

Breeding events manipulated for other studies and re-nesting-attempts by focal females within the same season were excluded from the sample. Nests established prior to the start of annual monitoring were excluded if the time gap between successive laid eggs exceeded 14 days, which represents the maximum gap recorded during daily surveys (Ortega, unpublished data). Such a large gap could indicate non-consecutive eggs, such as 1st and 3rd eggs, implying that not all eggs had been monitored.

Critical time windows

Using a sliding window approach, implemented in the *climwin* R package (Bailey & De Pol, 2016; van de Pol et al., 2016), we fitted Poisson GLMMs and searched for time periods (start and end dates of the weather signal), statistics (e.g., average, minimum, and maximum), and functions (linear or quadratic expression) of the 4 proxies of ocean primary productivity that were more associated with clutch size. Before implementing the sliding window approach, a base model (that is, a model with no weather signal) was selected amongst four competing Poisson GLMMs, that accounted for differences in clutch size (Table S1). All competing models included laying date (standardised by setting November 3rd as day 1) and a binary categorical variable denoting whether the clutch was established prior to or during monitoring (hereafter establishment timing). Additionally, the linear and quadratic expression of the focal female's and her partner's ages were tested singly and jointly. The four competing models were ranked based on their Akaike Information Criterion corrected for small samples (AICc). The model with the smallest AICc and fewest parameters was considered the best supported (Table S1). Laying date accounted for the higher breeding output of early breeders compared to late-breeders (Peña, 2009), while establishment timing accounted for potential underestimation of sizes of clutches established prior to the start of monitoring, when lost eggs could not be tallied. The quadratic expression of age was added to account for reproductive senescence, which occurs in this population after age ~10 years (Beamonte-Barrientos et al., 2010; Velando, Drummond, et al., 2006). The male's age was included as females are known to adjust their breeding effort in response to their partners' condition, indicated by foot hue (Velando, Beamonte-Barrientos, et al., 2006). Unmeasured environmental effects such as air temperature and population density (Ancona & Drummond, 2013) were controlled by including the current year as a random effect. Additionally, both the focal female's and her partner's identity were included as random effects to account for statistical non-independence between observations.

Climwin fitted a predetermined number of models, based on the statistics and functions, and ranked them by their AICc. To estimate the probability (p) of obtaining a false positive, the same sliding window approach was applied to 100 randomizations of the original weather data. A signal was considered reliable when p was < 0.05. Since female boobies initiate their clutches throughout the boreal seasons (Ortega et al., 2022), the time windows were defined relative to each female's laying date, as opposed to a fixed calendar date for the entire population (Hidalgo Aranzamendi et al., 2019; van de Pol et al., 2016). Climwin was set to evaluate all weekly windows going back as far as 24 weeks (~5.5 months) before clutch initiation. The summary of all tested sets of climate window parameters is provided in Table S2 (*Apéndice* I) of the Electronic Supplementary Material.

Plasticity in clutch size in response to proxies of prey availability

Bayesian methods were used to refit the best-supported time window GLMM. To assess individual-level reaction norms for clutch size in response to the best supported weather signal, a random regression mixed model (RRMM) was employed (Box 1). RRMMs enable estimation of the correlation between individual-specific intercepts and slopes, providing insights, for example, into whether females with higher median trait values exhibit more (or less) positive slopes in response to a weather signal (Arnold et al., 2019).

Box 1. Random regression mixed model formula.

$$y_{ij} = \alpha + \beta x_j + a_i + b_i x_j + e_{ij}$$

Where y_{ij} denotes the phenotypic trait value of the individual i on year j; α and β are fixed effects of the overall intercept (the population median phenotype if x is mean-centred) and slope regression coefficients, respectively; x_j is the environmental signal experienced on year j (median centred); a_i is the random effect with the random intercept coefficient for individual i (which represents the difference in medians between individuals), b represents the random slope or individual-specific slope for the individual i in response to the environmental signal x in the year j, and e_{ij}, being the residual for individual i on year j. The random regression component of the equation estimates individual-level intercepts (a) and slopes (b), relative to the fixed effects at the population level.

A model selection procedure identified the best-supported model amongst the GLMM and the RRMM. For this procedure, the leave-one-out cross-validation information criterion (LOO-IC) was computed to estimate the expected log predictive density (ELPD), which quantifies the predictive fit of a model. The model with the highest ELPD value was selected (Hollenbach & Montgomery, 2020). If the difference in ELPDs between the best-supported model and the subsequent competing model was not at least twice the size of the estimated standard error (SE) of this difference, the models were considered equivalent (Hollenbach & Montgomery, 2020), and the most parsimonious one was chosen. LOO-IC and ELPD were estimated using the *loo* package (Vehtari et al., 2017).

Selection on clutch size

The best-supported Bayesian model was incorporated as a sub-model in a multivariate generalized model with group-specific terms (MVGLM). MVGLMs handle multiple dependent variables and estimate the correlation between group-specific terms or random effects across different sub-modes within the GLM framework (q.v., Arnold et al., 2019; c.f., Boulton et al., 2018). The MVGLM comprised three GLMM sub-models, with clutch size (the best-supported model from the previous step), annual number of fledglings produced (hereafter, fledging success), and annual mortality of the female as dependant variables (a binary outcome, 0= survive to next event or 1= was not resighted again). Poisson GLMMs were fitted for the clutch sizer and fledging success sub-models, while a Binary GLMM was fitted for the females' annual mortality sub-model. Each sub-model included focal female identity and current year as group-specific terms. Since the *stan_mvmer* function from the R package *Rstanarm* (Gabry, Ali, et al., 2022) only estimates the correlation between two random effects, the males' identity was omitted from all sub-models. In the sub-model for fledging success, laying date was included as fixed effect due to its strong correlation with current weather conditions and the proportion of nestlings predated by snakes (Ortega et al., 2021, 2022). Finally, the sub-model for annual mortality incorporated age at first reproduction and female age as fixed effects, the former controlling for selective appearance (van De Pol & Verhulst, 2006) and the latter accounting for the relationship between age and probability of dying.

Results

Environmental conditions around Isla Isabel

Between 2012 and 2022, notable trends emerged in the average concentrations of chlorophyll-α ([Chl- α]), particulate organic carbon ([POC]), and the diffuse attenuation coefficients at a wavelength of 490 nm (KD490), composing a consistent pattern within the waters encircling Isla Isabel during throughout the blue-footed booby reproductive season. These proxies of ocean primary productivity collectively displayed a shared trajectory, with an increase from November to March followed by a gradual descent terminating in July (Table 1). Average sea surface temperatures (SST) showed an inverse pattern, beginning at 28.77 °C with a mean absolute deviation (MAD) of 0.79 °C in November, steadily decreasing to 23.71 °C (MAD= 1.05 °C) in March, then progressively increasing up to 29.96 °C (MAD = 0.58 °C) in July (Table 1).

Table 1. Seasonal variation of average environmental condition (2012-2022)

Month	[Chl- α] (MAD) mg m^{-3}	[POC] (MAD) mg m^{-3}	KD490 (MAD) m^{-1}	SST (MAD) °C
November	0.47 (0.19)	96.44 (24.48)	0.06 (0.01)	28.77 (0.79)
December	0.45 (0.14)	99.44 (22.45)	0.06 (0.01)	26.25 (0.87)
January	0.70 (0.33)	138.06 (48.34)	0.08 (0.02)	24.67 (0.95)
February	0.66 (0.33)	124.43 (37.73)	0.08 (0.02)	24.25 (0.93)
March	0.86 (0.57)	142.65 (59.10)	0.09 (0.04)	23.71 (1.05)
April	0.54 (0.22)	115.37 (35.29)	0.07 (0.01)	24.89 (0.87)
May	0.59 (0.26)	116.49 (33.73)	0.07 (0.01)	26.77 (0.79)
June	0.41 (0.14)	93.67 (19.61)	0.06 (0.01)	28.03 (0.96)
July	0.36 (0.13)	85.89 (18.85)	0.05 (0.01)	29.96 (0.58)

Mean absolute deviations (MAD) are provided.

Over the span of a decade, from 2012 to 2022, there were distinctive fluctuations in the annual averages of [Chl- α], KD490, and SST, characterized by a non-linear trajectory (Table 2). The behaviour of both [Chl- α] and KD490 followed a U-shaped pattern, declining from 2012 to 2017, then increasing up to 2022 (Table 2a-c; Figure 2a-c). Conversely, SST exhibited an inverted U-pattern, undergoing progressive increase from 2012 to 2015, followed by gradual decline thereafter. Notably, the annual averages of POC exhibited a steady consistency throughout this timeframe (Table 2b).

Table 2. Fluctuations in yearly average environmental conditions between 2012 and 2022.

a) Chlorophyll-α concentration

Parameter	Median	MAD SD	HPD 89%		Random effects	SD	n
			Lower	Upper			
Intercept	**0.427**	**0.094**	**0.265**	**0.573**	Year (Intercept)	0.126	11
Time	-0.121	0.096	-0.281	0.040	Residual	0.229	
Time^2	**0.410**	**0.216**	**0.052**	**0.770**			
Season [a]							
Winter	**0.187**	**0.098**	**0.023**	**0.344**			
Spring	0.038	0.098	-0.115	0.206			
Summer	-0.042	0.098	-0.203	0.117			

b) Particulate organic carbon

Parameter	Median	MAD SD	HPD 89%		Random effects	SD	n
			Lower	Upper			
Intercept	**112.356**	**6.425**	**101.576**	**123.168**	Year (Intercept)	16.630	11
Time	-0.148	1.006	-1.748	1.433	Residual	30.110	
Time^2	0.055	1.015	-1.580	1.644			
Season [a]							
Winter	0.273	0.998	-1.273	1.896			
Spring	0.005	0.998	-1.579	1.575			
Summer	-0.172	0.978	-1.699	1.456			

c) Diffuse attenuation coefficients at a wavelength of 490 nm

Parameter	Median	MAD SD	HPD 89%	Random effects	SD	n

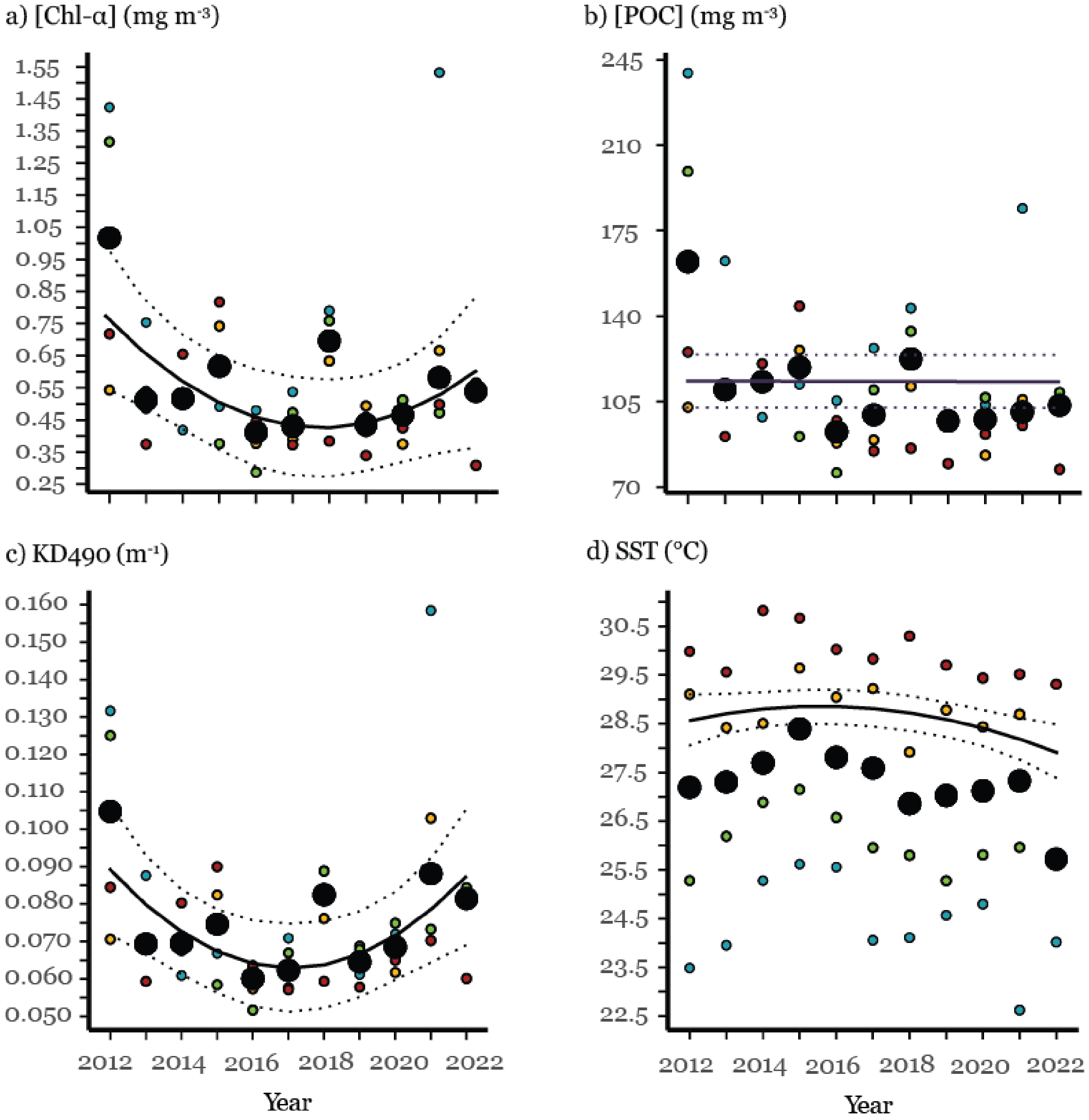
			Lower	Upper			
Intercept	**0.062**	**0.007**	**0.050**	**0.074**	Year (Intercept)	0.009	11
Time	-0.002	0.007	-0.015	0.010	Residual	0.018	
Time^2	**0.041**	**0.016**	**0.014**	**0.070**			
Season [a]							
Winter	**0.013**	**0.008**	**0.001**	**0.026**			
Spring	0.003	0.008	-0.009	0.015			
Summer	-0.004	0.008	-0.017	0.008			

d) Sea surface temperature

Parameter	Median	MAD SD	HPD 89%		Random effects	SD	n
			Lower	Upper			
Intercept	**28.804**	**0.224**	**28.435**	**29.157**	Year (Intercept)	0.320	11
Time	-0.392	0.235	-0.769	0.011	Residual	0.538	
Time^2	**-0.922**	**0.480**	**-1.718**	**-0.143**			
Season [a]							
Winter	**-4.093**	**0.232**	**-4.486**	**-3.726**			
Spring	**-2.450**	**0.226**	**-2.812**	**-2.071**			
Summer	**1.325**	**0.223**	**0.964**	**1.689**			

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] Autumn was used as reference level.

Figure 2. Interannual variation in average environmental conditions from 2012 to 2022.



Large black dots represent annual means; small and coloured dots represent seasonal means. The black solid lines represent the slope and associated 89% highest posterior density interval (shown in dotted lines) of linear mixed regressions of average environmental conditions on year.

Clutch size adjustments

For 1203 females that reproduced between 2013 and 2022, the model of minimum [Chl- α] was identified as the best-supported critical window, spanning the 5 weeks leading up to the laying of the first egg (ΔAICc =-8.06 compared to the null model; Table 3 and S2). Notably, the critical windows for minimum [POC] and minimum KD490 were also supported, (ΔAICc =-7.42 and ΔAICc = -7.79 compared to the null model, respectively). These timeframes exhibited comparable durations, minimum [POC] being one week shorter, and showed a strong correlation with [Chl- α] (r = ~0.90; Table 3). On other hand, the models containing SST values were less supported (ΔAICc =-5.5 compared to the null model) and exhibited wider critical windows (spanning ~3.6 months). Finally, no age-related effects on clutch size were supported (Table S1).

Table 3. Top 10 critical window models.

Model	Environmental condition	Statistic	Function	ΔAICc	Window opens	Window closes	$P_{\Delta AICc}$
1	**Chl-α**	**min**	**lin**	**-8.06**	**5**	**0**	**<0.001**
2	KD490	min	lin	-7.79	5	0	<0.001
3	POC	min	lin	-7.42	4	0	<0.001
4	Chl-α	min	quad	-6.16	4	0	<0.001
5	Chl-α	mean	lin	-5.94	6	0	<0.001
6	KD490	min	quad	-5.83	5	0	<0.001
7	SST	max	lin	-5.5	20	4	<0.001
8	POC	min	quad	-5.42	4	0	<0.001
9	KD490	mean	lin	-5.36	4	1	<0.001
10	Chl-α	max	quad	-4.96	6	2	<0.001

Best-supported critical window is presented in bold. For all models, ΔAICc denote the difference in AICc scores between the current model and a null model (i.e., a model without a climate signal), and $P_{\Delta AICc}$ values denote the probability that the climate signal is a false positive. For all environmental conditions, three statistics (mean, maximum, and minimum) along with their lineal and quadradic functions were tested.

The median clutch size increased from 1.69 eggs at [Chl-α] = 0.15 mg m^{-3} up to 2.41 eggs at [Chl-α] = 1.03 mg m^{-3} (Table 2a; Figure 3a). Similarly, the median clutch size increased from 1.71 at [POC] = 56.38 mg m^{-3} up to 2.18 at [POC] = 167.19 mg m^{-3} (Table 2b; Figure 3b). Additionally, a similar correlation between laying date and clutch size was detected in the models that included [Chl-α] and [POC] as independent variables: median clutch size decreased from ~2.12 eggs for clutches established in late-November down to ~1.56 eggs for those in early-July (Table 2; Figure 3c). Notably, despite being highly correlated with [Chl-α], the effect of KD490 on clutch size was found to be inconclusive (Table S3).

Table 4. Clutch size adjustment of 1203 females in response to a) minimum phytoplankton chlorophyll-α concentration and b) minimum particulate organic carbon concentration.

a) Chlorophyll-α concentration

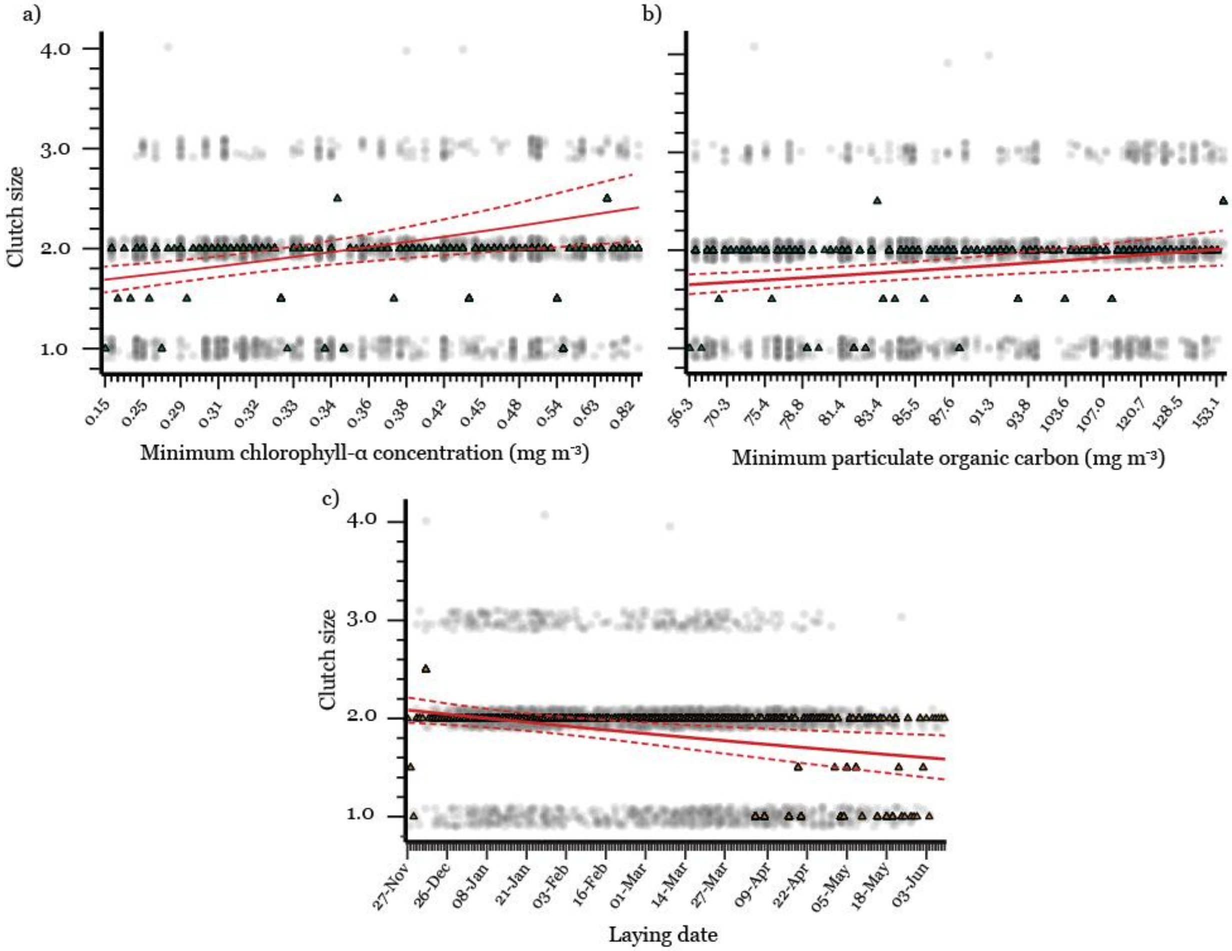
Parameter	Median	MAD SD	HPD 89%		Random effects	SD	n
			Lower	Upper			
Intercept	**0.621**	**0.037**	**0.563**	**0.68**	Female ID (Intercept)	0.016	1203
[Chl-α]	**0.092**	**0.03**	**0.042**	**0.139**	Male ID (Intercept)	0.016	1316
Laying date	**-0.109**	**0.041**	**-0.174**	**-0.041**	Year (Intercept)	0.027	9
Establishment timing [a]							
During the survey	-0.003	0.045	-0.074	0.069			

b) Particulate organic carbon

Parameter	Median	MAD SD	HPD 89%		Random effects	SD	n
			Lower	Upper			
Intercept	**0.623**	**0.036**	**0.563**	**0.679**	Female ID (Intercept)	0.012	1203
[POC]	**0.088**	**0.031**	**0.039**	**0.137**	Male ID (Intercept)	0.015	1316
Laying date	**-0.102**	**0.040**	**-0.166**	**-0.036**	Year (Intercept)	0.027	9
Establishment timing [a]							
During the survey	-0.006	0.044	-0.076	0.066			

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] Nests established prior to the initial survey were used as reference level.

Figure 3. Clutch size adjustment in response to concentration of a) chlorophyll-α, b) particulate organic carbon, and c) laying date [a].



Median effects and their 89% highest posterior density intervals (shown in dotted lines) are presented in red; triangles represent median clutch sizes at each value while vertically jittered dots are raw observations of clutches. [a] The depicted slope and associated 89% HPD derived from the generalized linear mixed regression evaluating the correlation between clutch size and chlorophyll-α.

Variation in individual plasticity in clutch size

Variation among individuals in clutch size plasticity in response to [Chl-α] and [POC] was not supported (Table 5). Thus, all females tended to adjust their clutch size to [Chl-α] and [POC] in a similar manner (Figure 3). (Table 4). Finally, inter-annual variation in clutch sizes across 9 years (2013 – 2022) was also low (Table 4)

Table 5. Model selection summaries

a) Chlorophyll-α			
Model	ELPD (±SE)	LOO-IC (±SE)	Δ ELPD (±SE)
GLMM	**-3477.3 (7.6)**	**6954.6 (15.1)**	**0.0 (0.0)**
RRMM	-3477.3 (7.6)	6954.6 (15.1)	0.0 (0.0)
b) Particulate organic carbon			
Model	ELPD (±SE)	LOO-IC (±SE)	Δ ELPD (±SE)
GLMM	**-3477.6 (7.6)**	**6955.2 (15.2)**	**0.0 (0.0)**
RRMM	-3477.6 (7.6)	6955.3 (15.2)	0.0 (0.0)

Most parsimonious models are in bold. The Estimated Log-Posterior Densities (ELPD), and Leave-one-out Information Criterion (LOO-IC), along with the differences (Δ) between models' ELPDs are highlighted are provided. Estimated standard errors (SE) for all statistics are shown in parenthesis.

Selection on clutch size

Among 1203 females observed across 9 years, individual median clutch sizes were not correlated with individual median fledging success or with females' annual mortality (Table 6). Females with above median clutch sizes did not produce more fledglings in a given year than their counterparts with smaller clutch sizes (Table 6), nor did they have higher annual mortality (Table 6). However, a moderately positive correlation (Table 6) was observed between individual fledging success ((annual number of fledglings produced) and annual mortality, implying a cost of reproduction: females with above-average fledging success had an above-median annual probability of not being re-sighted (Table 6).

The median clutch size was of 1.863 eggs with a median absolute deviation (MAD) of 0.038 eggs. Females produced a median of 0.455 fledglings with a MAD of 0.19 fledglings, and their median annual mortality was 33.2% with a MAD of 0.010%.

Table 6. Correlation between group-specific terms across sub-models assessing a) clutch size, b) fledgling success, and c) annual mortality of 1203 females across 9 years.

Environmental condition	I) Chlorophyll-α			II) Particulate organic carbon		
Random effects						
Female ID	SD	Correlation		SD	Correlation	
a) Clutch size (Intercept)	0.016	-		0.016	-	
b) Fledging success (Intercept)	0.067	0.06 $^{a/b}$		0.068	0.02 $^{a/b}$	
c) Annual mortality (Intercept)	0.981	-0.01 $^{a/c}$	0.26 $^{b/c}$	0.989	-0.01 $^{a/c}$	0.32 $^{b/c}$
Year						
a) Clutch size (Intercept)	0.029	-		0.031	-	
b) Fledging success (Intercept)	1.126	0.20 $^{a/b}$		1.110	0.24 $^{a/b}$	
c) Annual mortality (Intercept)	1.897	-0.03 $^{a/c}$	0.11 $^{b/c}$	1.923	0.00 $^{a/c}$	0.13 $^{b/c}$
Dependent variables						
a) Clutch size						
Parameter	Median	MAD SD		Median	MAD SD	
Intercept	0.618	0.036		0.62	0.037	
Concentration	0.091	0.03		0.088	0.03	
Laying date	-0.111	0.04		-0.102	0.04	
Nest establishment						
During the survey	0.001	0.044		-0.003	0.045	
b) Fledging success						
Parameter	Median	MAD SD		Median	MAD SD	
Intercept	-1.377	0.334		-1.385	0.321	
Laying date	-1.806	0.098		-1.806	0.100	
c) Annual mortality						
Parameter	Median	MAD SD		Median	MAD SD	
Intercept	-0.670	0.560		-0.671	0.551	
Age at first reproduction	0.332	0.100		0.330	0.100	
Female age	0.867	0.130		0.872	0.133	

The pairwise correlations between specific random effects are specified by a superscript dash. MAD median absolute deviation.

Discussion

The study aimed to examine the life history impacts of breeding effort adjustments in the Blue-footed booby (*Sula nebouxii*), a neotropical seabird, in relation to environmental variation. Particularly, we investigated the relationship between clutch size and key indicators of ocean primary productivity, which provide information on the availability of seabirds' prey (Gusmao et al., 2022; Szostek & Becker, 2015; Weimerskirch et al., 2005), including chlorophyll-α (Chl-α), particulate organic carbon (POC), and diffuse attenuation coefficients at a wavelength of 490 nm (KD490), along with sea surface temperature (SST). By analysing 9 years of reproductive data, we discovered a population-wide adjustment of clutch size in response to ocean primary productivity. Particularly, females increased their clutch sizes when concentrations of Chl-α and POC in surface waters prior to the onset of laying increased. Finally, we found that between-female variation in clutch sizes was low and did not substantially impact yearly production of fledglings or annual mortality of females.

Environmental conditions around Isla Isabel

A consistent pattern was observed in the temporal trends of [Chl-α], [POC], and KD490 within the waters encircling Isla Isabel. Together, these proxies revealed a shared trajectory characterized by distinct seasonal variation. From November to March, there was a noticeable increase in their average values, followed by a gradual decline culminating in July. In contrast, SST followed an inverse pattern, with temperatures declining from November to March and then progressively increasing until July. Collectively, these dynamics imply a heightened level of ocean primary productivity during the November-March period when most boobies lay and hatch their first eggs (Ortega et al., 2022), suggesting synchronisation of these birds with the seasonal oscillation of ocean primary productivity.

Examining the decade-long trends in annual averages affirmed previously reported ocean-atmosphere dynamics (Ortega et al., 2021). The U-shaped trajectories observed in both [Chl-α] and KD490, marked by an initial decline followed by subsequent increases from 2012 to 2022, align with the SST inverted U-pattern, initially ascending from 2012 to 2015 and then gradually descending. These trends could be propelled by larger-scale oceanic and atmospheric phenomena, such as the El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (Hu & Fedorov, 2019; Mantua & Hare, 2002; Yasunaka et al., 2022). Meanwhile, the consistent annual averages of POC over the decade underscore its inherent stability, suggesting a resilient organic carbon supply to the ecosystem. Importantly, this resilience holds true even in the face of fluctuations in the planktonic trophic structure. Such shifts, driven by factors such as sea surface temperature, do not hinder the consistent production of particulate organic carbon (POC). This uninterrupted POC production can be attributed to the combined contributions of bacterial and phytoplankton sources (Guenther et al., 2008).

Clutch size adjustments

Minimum [Chl-α] and [POC] during the 5 and 4 weeks, respectively, prior to the laying of females' first eggs were found to be correlated with their clutch sizes. Seemingly, higher [Chl-α] and [POC] values prior to laying indicate higher prey availability, prompting an increase in clutch size. This pattern has been observed in other animals, such as captive-bred females of the viviparous checkered garter snake (*Thamnophis marcianus*), which increase litter size by up to 40% in response to a high-energy diet (Ford & Seigel, 1989). Likewise, early-nesting boobies of a more northern population feeding on prey with high lipid and caloric content such as Pacific anchovetas (*Cetengraulis mysticetus*) and Pacific thread herrings (*Opisthonema libertate*) laid larger clutches than boobies that fed on prey with both lower lipid and caloric content such as Blue mackerels (*Scomber australasicus*) and Californian anchovies (*Engraulis mordax*)(González-Medina et al., 2018). Hence, female blue-footed boobies faced with abundant food may invest more in their current reproduction by increasing their clutch size. However, a more in-depth exploration of their connection to the nutritional composition of the prey is warranted. Investigating whether one of these proxies of primary ocean productivity correlates with a high-energy diet conducive to higher breeding investment could unveil pivotal insights.

The progressive decrease in clutch size observed in the boobies over the course of their breeding season may be influenced by the perceived risk of clutch predation. Predation risk can influence the behaviours and life-history decisions of prey species (Lima, 2009). For instance, the Siberian jay *Perisoreus infaustus*, reduces its clutch size in response to heightened nest predation risks posed by corvids, which prey on both eggs and nestlings (Eggers et al., 2006). Therefore, the apparent seasonal increase in the presence and activity of seagulls, the only egg predator in the colony, may have prompted a seasonal decrease in the current reproductive effort of the boobies, resulting in smaller clutches later in the season.

In female blue-footed boobies, plasticity in clutch size with respect to proxies of prey availability is a population-wide phenomenon. Despite the wide range of environmental conditions experienced by individuals both within and between years, substantial variation between females in their response to proxies of prey availability was lacking. This pattern echoes findings in other species. For instance, studies on red deer (*Cervus elaphus;* Froy et al., 2019), big horn sheep (*Ovis canadensis;* Renaud et al., 2019), common guillemots (*Uria aalge;* Reed et al., 2006), and common terns (*Sterna hirundo*; Dobson et al., 2017) have also failed to detect individual variation in plasticity, albeit in phenological traits. The lack of individual variation in plasticity in clutch size in the blue-footed boobies may stem from stabilizing selection. This mechanism could work against individuals deviating from the median population response to proxies of prey availability (e.g., Reed et al., 2006). Furthermore, the population's tendency to forego reproduction during years of extremely low food availability (Ancona & Drummond, 2013), like in 2016 when an extreme El Niño occurred (Hu & Fedorov, 2019; Santoso et al., 2017), coupled with the lack of correlation between clutch size and individual annual mortality (as indicated in this study), suggests that females adaptively buffer their longevity. While the blue-footed boobies' adjustments of clutch size in response to proxies of prey availability may appear adaptive, it could also be neutral in terms of fitness implications: prey availability may constrain body condition, limiting current reproductive effort without directly affecting and individual's fitness, as shown in this study.

In this study, we showed that female blue-footed boobies from a population off the Pacific Coast of Mexico exhibited remarkably consistent adjustments in breeding effort in response to environmental variation. These long-lived birds may optimize their fitness by adjusting their clutch sizes in response to prey availability prior to laying because it predicts subsequent availability. Our findings provide valuable insights into the strategies employed by wild populations to accommodate to environmental conditions. Moreover, they suggest that blue-footed boobies' plasticity may make them be resilient to climate change and reduced prey availability within the range of values experienced between 2013 and 2022, but cannot tell us how boobies will respond to more extreme values. Furthermore, comprehensive understanding of the consequences of environmental shifts on population dynamics will require integrative exploration of how animals adjust their physiology, behaviours, and life histories in response to environmental variation.

Author Contributions

Santiago Ortega: Conceptualization, Investigation, Original draft, Methodology, Formal analysis, Data presentation. **Loeske Kruuk:** Statistical analyses, Revision of manuscript. **Cristina Rodríguez**: Investigation, Revision of manuscript, Data recording and curation. **Hugh Drummond**: Investigation, Data recording, Funding, Revision of manuscript, Administration, Supervision of project.

Data Availability

All data analysed in this study are included as Supplementary material.

Declaration of Interests

We declare no conflict of interest.

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Capítulo 2.

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 old. 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 (Bathiany et al., 2018; Corlett, 2012; Kusunoki et al., 2020; Thornton et al., 2014), along with more extreme weather events (Stott, 2016). By increasing the frequency of reproductive failure or reducing nestling and adult survival, both seasonal and intra-annual weather variations can potentially influence avian population dynamics (Moreno et al., 2011).

Breeding investment and reproductive 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 & 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).

It is well documented that some birds can modify the timing of reproduction to avoid unfavourable conditions and even match their food phenology (Charmantier & 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 & 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., 2008b), 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 & 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 & Dingemanse, 2020). In the White stork (*Ciconia ciconia*), a long-lived bird that also modifies its laying date in response to weather conditions: 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 (Sin Yeon Kim et al., 2007; Osorio-Beristain & Drummond, 1998) 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 (Lluch-Cota et al., 2017; Morales-Bojórquez et al., 2003), 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 (Anctil et al., 2014; Bionda & Brambilla, 2012).

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 & 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 ± SD) through chick fledging (~70 days old). The reproductive phenology of the population on Isla Isabel is highly asynchronous (Figure 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).

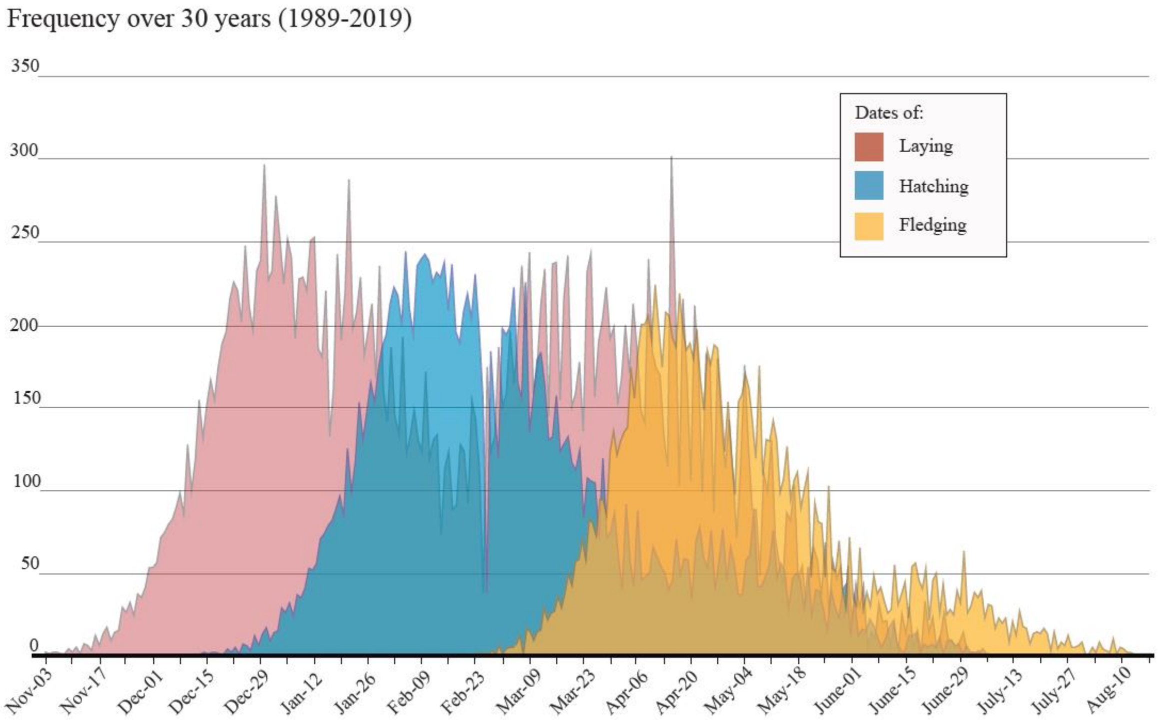

Figure1. Breeding phenology of the blue-footed booby on Isla Isabel. Dates of 29,147 first laid-eggs, 16,255 hatched eggs, and 12,422 fledged chicks across 31 reproductive seasons from 1989-2019.

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 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; Sin Yeon 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 x 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 x 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 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 70d-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 (± 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 1) body mass and ulna length were available. For 21 reproductive years, mean weight, and ulna length at 70d 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, 2022). All independent variables were standardized prior to model fitting to facilitate the interpretation of parameter estimates (Cade, 2015; Grueber et al., 2011). 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 & 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 1) hatching success and 2) fledging success, and for every fledgling 3) its body condition at 70d. 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 (Figure 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 & 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 (Hidalgo Aranzamendi et al., 2019; van de Pol et al., 2016). 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:

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

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 10000 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, Ali, et al., 2022) and *shinystan* (Gabry, Veen, et al., 2022), 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 (mean ± standard deviation) in November to 24.21±1.57 °C in February, then gradually increased to 31.28± 0.98 °C in August (Figure 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; Figure 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.

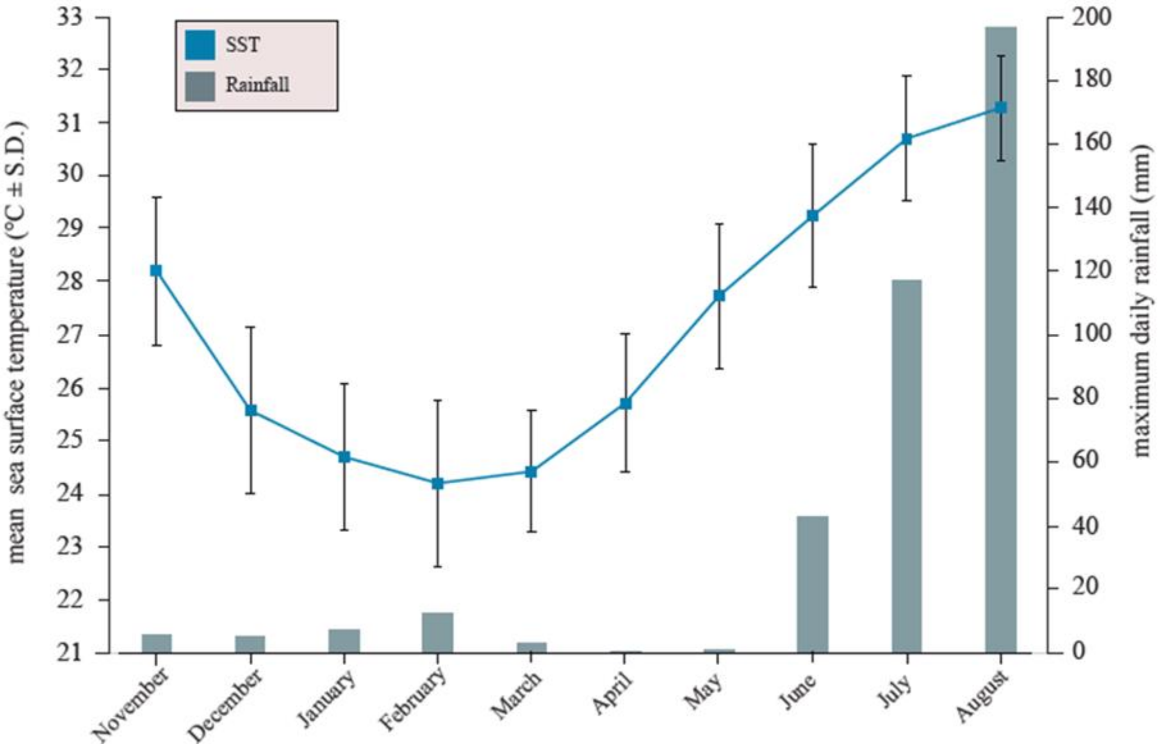

Figure 2. Weather conditions on Isla Isabel and its surrounding waters (1988-2019).

Hatching success

For 2441 incubated clutches, only sea surface temperature explained variation in the proportion of eggs that hatched. Mean SST between the 1st week of each pair's pre-laying period and their fifth week of incubation –a week prior to hatching– (Apéndice II S1a; Figure 3a) affected hatching success in a nonlinear manner (table 1a, Figure 3b). The proportion of eggs that hatched was roughly 37% when mean SST was 21.5°C, increasing up to 44% between 22.5 - 24.5°C, then progressively declined to 3% at >29.5°C (Figure 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): later breeders experience warmer mean SSTs (Pearson's correlation: $r = 0.76$, $p = <0.00$).

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*			
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. *Clutches of one egg were used as reference level.

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 (Apéndice II Table S1b, Figure 3a) positively affected their fledging success (table 2, Figure 3c). Fledging success progressively increased from 55% at ~0 mm of rain up to ~87% between 16-24 mm of rain. Fledging success was also affected by brood size: 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: late breeders experienced drier conditions (Pearson's correlation: r = -0.58, p= <0.00).

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*				
	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* stands for median absolute deviation. *Nests rearing only one chick were used as reference level.

Fledgling body condition

Body condition of 507 fledglings from 409 nests correlated only with SST. Mean SST between the 1st week of the pre-laying period and the 9th week of rearing –a week before reaching 70d– (*Apéndice* II Table S1c; Figure 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: Figure 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: 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*		
2nd	**-0.025**	**[-0.042, -0.006]**
3rd	**-0.146**	**[-0.214, -0.076]**
Brood size**		
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. *First hatched chicks and **nests rearing only one chick were used as reference levels.

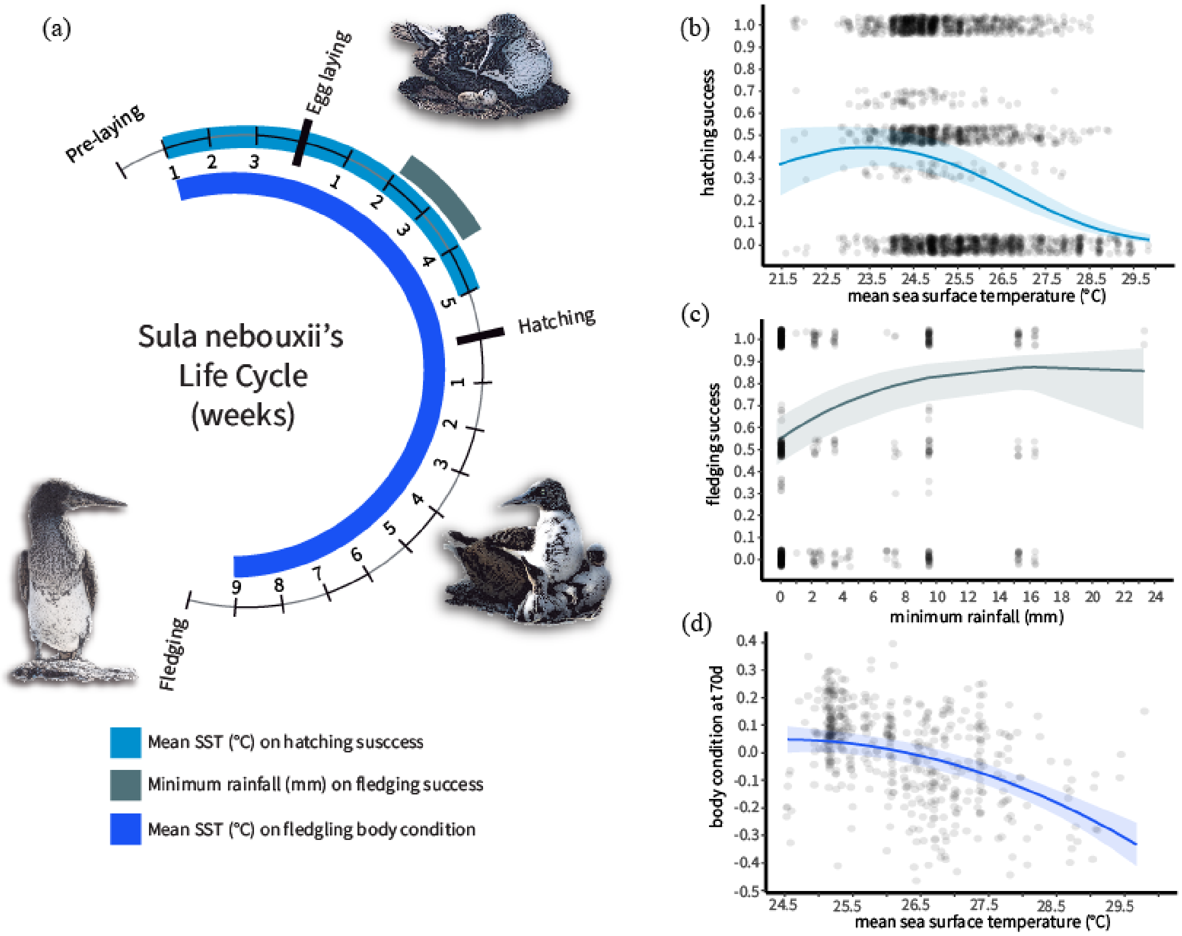

Figure 3. (a) Critical time windows of SST and rainfall during the boobies' reproduction. Effects of (b) mean SST on hatching success, (c) minimum rainfall on fledging success, and (d) mean SST on fledgling body condition. Median effects of each weather condition and their 89% highest posterior density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

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 ± S.D.), respectively, and the average body condition for 21 years was 0.00 ± 0.15. Annual robust coefficient of variation ($\mathrm{RCV}_{\mathrm{M}}$) 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 were explained by the RCV_{M}s of minimum rainfall and mean SST, respectively (Table 4b-4c).

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.

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 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 1st 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 inter-annual 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: 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 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 (Boyce et al., 2006; Jean-Michel Gaillard et al., 2003). 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 2nd to 4th weeks of incubation increased the proportion of chicks that fledged while high mean SSTs present during the 1st week of the pre-laying period to the 9th 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 & 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: 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 (Figure 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 (Bravo-Cabrera et al., 2017; Magaña et al., 2003). 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): 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 0-5 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 (Corlett, 2012; Williams et al., 2007), 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.

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Declarations

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Consent to participate. Not applicable.

Consent for publication. Not applicable.

Availability of data and material. 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.

Authors contributions. SO conceptualized the idea, SO and CR curated the data, HD and CR collected the data, SO wrote the original draft, CR and HD reviewed and edited the manuscript, SO performed the statistical analyses.

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Discusión general

Esta investigación tuvo como objetivo estudiar los ajustes en historia de vida de las hembras de una población de bobos de patas azules (*Sula nebouxii*) en respuesta a indicadores de productividad primaria del océano (PPO), los cuales proporcionan información sobre la disponibilidad de sus presas (Gusmao et al., 2022; Szostek & Becker, 2015; Weimerskirch et al., 2005). En primer lugar, analicé nueve años de datos demográficos para determinar 1) si las hembras exhiben plasticidad en su tamaño de puesta en respuesta a cuatro variables de PPO, y 2) si dicha plasticidad está bajo selección. Posteriormente, evalué 32 años de datos reproductivos para examinar los efectos de las variables meteorológicas sobre el éxito de eclosión y emplumado, y la condición corporal de la progenie al emplumar (rasgos empleados como sucedáneos de inversión parental). Finalmente, analicé si los años con mayor estabilidad ambiental, es decir, con menos variabilidad meteorológica, eran menos exitosos que los años con mayor variabilidad ambiental.

Plasticidad en tamaño de puesta

Las hembras de bobo de patas azules aumentaron el tamaño de sus puestas cuando aumentaron las concentraciones tanto de clorofila-α como de carbón orgánico particulado (POC, por sus siglas en inglés) en las aguas superficiales alrededor de Isla Isabel antes del inicio de la reproducción. Además, encontré que la variación entre hembras en el tamaño de la puesta fue baja y no afectó sustancialmente la producción anual de emplumados ni la mortalidad anual de las progenitoras, en otras palabras, no afectó sus trayectorias de historia de vida.

La concentración mínima de clorofila-α y POC durante las cinco y cuatro semanas previas, respectivamente, a la puesta del primer huevo de cada hembra se correlacionó con el tamaño de su puesta. Valores más altos de clorofila-α y POC durante este período, indicando probablemente una mayor disponibilidad de presas, llevaron a un aumento en el tamaño de la puesta. Esta plasticidad en el esfuerzo reproductivo en respuesta a los recursos cambiantes no es exclusiva de los bobos de patas azules. Otros organismos, como las hembras –criadas en cautiverio– de la serpiente vivípara *Thamnophis marcianus*, también han mostrado un aumento en el tamaño de la camada cuando se les proporciona una dieta alta en energía en comparación con aquellas con una dieta baja en energía (un aumento de >40%; Ford & Seigel, 1989). Un patrón similar se ha observado en los bobos de patas azules de una población más al norte de Isla Isabel (Isla El Rancho, Sinaloa, México; ~ 440 km al noroeste de Isla Isabel). En esta población norteña, las hembras que consumen presas con alto contenido de lípidos y calorías, como son las anchovetas del Pacífico *Cetengraulis mysticetus* y los arenques del Pacífico *Opisthonema libertate*, que son más abundantes al comienzo de la temporada de reproducción de estas aves, ponen puestas más grandes (2-3 huevos) que aquellas con una dieta baja en energía (González-Medina et al., 2018). Por lo tanto, cuando tienen comida abundante y/o de alta calidad nutricional, las hembras de los bobos de patas azules pueden invertir más en su reproducción actual aumentando el tamaño de su puesta.

La disminución progresiva del tamaño de la nidada observada en los bobos de la Isla Isabel a lo largo de la temporada de reproducción puede estar influenciada por el riesgo percibido de depredación de la puesta. Se sabe que el riesgo de depredación puede influir en el comportamiento y las decisiones de historia de vida de las especies presa (Lima, 2009). Por ejemplo, el arrendajo siberiano *Perisoreus infaustus* reduce el tamaño de su puesta en respuesta al aumento del riesgo percibido de depredación del nido (Eggers et al., 2006). Por lo tanto, el aumento estacional en la presencia y actividad de las gaviotas, los únicos depredadores de los huevos en la colonia de Isla Isabel, puede haber provocado una disminución estacional en el esfuerzo reproductivo actual de los bobos de patas azules, resultando en puestas más pequeñas más tarde en la temporada.

En las hembras de los bobos de patas azules, la plasticidad en el tamaño de la puesta con respecto a los indicadores de disponibilidad de presas es un fenómeno generalizado en la población. La falta de variación en la plasticidad individual en el tamaño de las puestas sugiere que las hembras respondieron de manera similar a las concentraciones de clorofila-α y POC. Además, las diferencias individuales en el tamaño de las puestas no proporcionaron ninguna ventaja en la producción de emplumados ni exacerbó la mortalidad anual de las progenitoras. Similar a lo que ocurre en la fenología del mérgulo común *Uria aalge*, la selección estabilizadora puede estar actuando en contra de los individuos que se desvían de la respuesta mediana de la población a los indicadores de disponibilidad de presas (Reed et al., 2006). Es importante mencionar que la plasticidad a nivel poblacional en el tamaño de las puestas en respuesta a los indicadores de disponibilidad de alimento podría ser adaptativamente neutral, ya que la disponibilidad de presas podría limitar la condición corporal y, por lo tanto, restringir el esfuerzo reproductivo actual. Sin embargo, la inclinación de la población a omitir años reproductivos durante períodos de disponibilidad extremadamente baja de alimento (Ancona & Drummond, 2013), junto con la ausencia de correlación entre la mortalidad anual de las progenitoras (este estudio), puede sugerir una estrategia de amortiguación en favor de su longevidad, y, por tanto, ser una respuesta adaptativa por parte de las hembras.

Ajustes de inversión parental a las condiciones meteorológicas

Encontré una correlación negativa entre la temperatura superficial del mar (*SST*, por sus siglas en inglés) promedio y el éxito en la eclosión. En particular, cuando los valores promedio de la SST superaron los 24.5°C desde tres semanas previas al establecimiento de la puesta y hasta la quinta semana de incubación, se observó una reducción en la proporción de huevos que eclosionaron. Patrón que coincide con un estudio anterior que informó del impacto negativo de aguas anormalmente cálidas en el éxito de eclosión en la misma población de estudio (Ancona et al., 2011). Amplié estos hallazgos al enfatizar el papel de las condiciones meteorológicas *in situ* en lugar de las desviaciones interanuales de SST de un período de referencia en el Pacífico Norte. Además, descubrí que SST promedio bajas (<21.5°C) cerca de Isla Isabel también tuvieron un efecto perjudicial, aunque pequeño, en el éxito de eclosión. Esto podría deberse a la reducción de la disponibilidad de alimento, ya que las floraciones de fitoplancton, de lo que se alimentan las presas principales de los bobos, requieren un calentamiento del agua para ocurrir (Trombetta et al., 2019).

No encontré un efecto negativo de las precipitaciones durante la incubación. En su lugar, hallé que las precipitaciones presentes durante la segunda a cuarta semana de incubación aumentaron la proporción de crías o polluelos que se emplumaron con éxito. Esto podría atribuirse al aumento de la abundancia de clorofitas en los mares costeros debido a los aportes de nutrientes de la lluvia (a través de la deposición de nutrientes atmosféricos o a través de la descarga de los ríos al mar; Kim et al., 2014; Thompson et al., 2015), lo que podría llevar a una mayor disponibilidad de presas para los bobos.

También encontré que altas SST promedio presentes durante la primera semana del período previo a la puesta y hasta la novena semana de crianza se asociaron con una menor condición corporal de las crías al emplumar. Las SST cálidas pueden indicar escasez de alimento tanto en el presente como en el futuro, lo que lleva a una reducción en la inversión parental actual en favor para futuras reproducciones. Este patrón se observa también en otras especies, donde las altas SST resultaron en menores tasas de provisionamiento o en la asignación de alimento de mala calidad a las crías (González-Medina et al., 2018; Tapper et al., 2020).

Tomando en cuenta los patrones previamente mencionados, propuse dos mecanismos potenciales mediante los cuales las condiciones atmosféricas *in situ* podrían influir en el éxito de eclosión y emplumado, y en la condición corporal de la progenie al emplumar. Primero, las condiciones atmosféricas y oceanográficas podrían afectar la disponibilidad de alimento y la condición corporal de los adultos, lo que lleva a una menor inversión reproductiva por parte de éstos. Segundo, estas condiciones atmosféricas podrían servir como una señal para que los padres ajusten sus decisiones de inversión en función de la disponibilidad anticipada de alimento para las crías. Ambos mecanismos coinciden con lo propuesto por la teoría de historia de vida, donde se espera que las especies longevas asignen recursos estratégicamente para hacer frente a entornos estresantes y optimizar su adecuación durante toda su vida (Boyce et al., 2006; Jean-Michel Gaillard et al., 2003).

Finalmente, encontré –contrario a lo esperado– que los años con SSTs promedio más estables antes y durante la etapa de incubación de cada pareja reproductora mostraron un mayor éxito de eclosión que los años con SSTs más variables durante este período. Entonces, las SSTs relativamente estables parecen estar fungiendo como como una señal confiable de la disponibilidad futura de alimento para los progenitores. La estabilidad de SSTs podría favorecer el ciclo natural de la PPO al permitir la acumulación de nutrientes en la superficie del mar (Chavez et al., 2011). Nutrientes que, a medida que avanza la temporada de reproducción y las SSTs aumentan, pueden desencadenar floraciones de fitoplancton, las cuales pueden ocurrir entre 0 y 5 días después de un aumento en las SSTs (Trombetta et al., 2019), y terminar atrayendo y alimentando a las presas de los bobos. Por otro lado, encontré evidencia débil e inconclusa sobre los efectos de la variabilidad anual en precipitaciones sobre el éxito de emplumado de las crías. La falta de conclusión en este hallazgo podría deberse al rango amplio de variación en los niveles de lluvia, lo cual puede ser atribuido a patrones meteorológicos estacionales, en particular, a la transición de las lluvias que acompañan el final de la temporada de huracanes, la cual termina en noviembre, a la temporada de secas que inicia en Marzo (CONANP, 2005). Por el contrario, el rango restrictivo en la variación de SST mínimas podría explicar la falta de conclusión sobre su efecto sobre la condición corporal de la progenie en el momento de emplumar. Aparentemente, los bobos de patas azules pueden criar a los juveniles solo cuando las SSTs promedio son relativamente estables, pero se requieren más datos morfológicos y anuales para confirmar esta aseveración.

Conclusión general

En este estudio se reveló que las hembras de los bobos de patas azules de la costa del Pacífico de México muestran ajustes consistentes en su esfuerzo reproductivo en respuesta a cambios ambientales. Estas aves, de larga vida, optimizan su adecuación ajustando su esfuerzo reproductivo según la disponibilidad de presas a través de su temporada reproductiva.

Esta tesis doctoral arrojó luz sobre las complejas relaciones entre las condiciones ambientales, principalmente aquellas que reflejan la PPO, y el éxito reproductivo de los bobos de patas azules. Al estudiar el impacto de las variaciones climáticas en rasgos de historia de vida clave, se proporciona información valiosa sobre las estrategias utilizadas por las poblaciones silvestres para adaptarse a las cambiantes condiciones ambientales. Estos hallazgos contribuyen al creciente cuerpo de investigación que permite entender las posibles respuestas de los animales silvestres frente al cambio climático y resaltan la importancia de futuras investigaciones para conservar y manejar adecuadamente las especies tropicales en el contexto del cambio ambiental global. Sin embargo, para comprender más a fondo los mecanismos regulatorios inferidos en este estudio, se necesitan observaciones directas del comportamiento, así como medidas fisiológicas, para evaluar cómo los bobos de patas azules modulan su inversión parental en respuesta a las condiciones ambientales. Además, estudiar cómo las condiciones ambientales afectan el fenotipo adulto de las crías supervivientes proporcionará información valiosa sobre los efectos a largo plazo del ambiente variable sobre la población.

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Apéndice I.

Table S1. Models investigating variation in clutch size ranked according to their relative support in the data, from best to worst.

Model	Parameters	k	loglik	AICc	ΔAICc	w_i
1	**Laying date + Establishment timing**	**6**	**-3478.70**	**6969.40**	**0.00**	**0.59**
2	Laying date + Establishment timing + Female age + Female age^2 + Male age + Male age^2	8	-3477.45	6971.0	1.52	0.27
3	Laying date + Establishment timing+ Female age + Female age^2	8	-3478.67	6973.40	3.97	0.08
4	Laying date + Establishment timing + Female age + Female age + Male age + Male age^2	10	-3477.33	6974.70	5.31	0.04

Best-supported model is presented in bold. *K* estimated number of parameters, *logLik* log likelihood, AICc Akaike Information criterion adjusted for small samples, ΔAICc difference in AICc scores between the current model and the most supported one, w_i Akaike wight. All models included current year, female ID, and male ID as random effects.

Table S2. Time window model selection. Evaluation of the most probable time windows of chlorophyll-α concentration ([Chl-α]), particulate carbon particle concentration ([POC]), diffuse attenuation coefficient at a wavelength of 490 nm (KD490), and sea surface temperature (SST) influencing clutch size.

Model	Environmental condition	Statistic	Function	ΔAICc	Window opens	Window closes	$P_{\Delta AICc}$
2	**CHL-α**	**min**	**lin**	**-8.06**	**5**	**0**	**<0.001**
14	KD490	min	lin	-7.79	5	0	<0.001
8	POC	min	lin	-7.42	4	0	<0.001
5	CHL-α	min	quad	-6.16	4	0	<0.001
1	CHL-α	mean	lin	-5.94	6	0	<0.001
17	KD490	min	quad	-5.83	5	0	<0.001
21	SST	max	lin	-5.5	20	4	<0.001
11	POC	min	quad	-5.42	4	0	<0.001
13	KD490	mean	lin	-5.36	4	1	<0.001
6	CHL-α	max	quad	-4.96	6	2	<0.001
19	SST	mean	lin	-4.86	2	2	<0.001

20	SST	min	lin	-4.86	2	2	<0.001
15	KD490	max	lin	-4.81	2	2	<0.001
3	CHL-α	max	lin	-4.79	2	2	<0.001
4	CHL-α	mean	quad	-4.62	6	2	<0.001
7	POC	mean	lin	-4.6	6	0	<0.001
10	POC	mean	quad	-4.52	21	14	<0.001
18	KD490	max	quad	-4.51	5	2	<0.001
16	KD490	mean	quad	-4.39	5	2	<0.001
9	POC	max	lin	-4.22	2	2	<0.001
24	SST	max	quad	-3.58	20	4	<0.001
12	POC	max	quad	-3.38	6	4	<0.001
22	SST	mean	quad	-3	24	16	<0.001
23	SST	min	quad	-2.92	2	2	<0.001

Best-supported critical window is presented in bold. For all models, ΔAICc denote the difference in AICc scores between the current model and a null model (i.e., a model without a climate signal), and $P_{\Delta AICc}$ values denote the probability that the climate signal is a false positive. If more than one model had the same ΔAICc values (or their difference was less than 2 AIC units), we considered them to be equivalent. When equivalent models were found, the most parsimonious one was selected. For all environmental conditions, three statistics (mean, maximum, and minimum) along with their lineal and quadradic functions were tested.

Table S3. Clutch size adjustment of 1203 females in response to diffuse attenuation coefficient at a wavelength of 490 nm (KD490)

Parameter	Median	MAD SD	HPD 89%		Random effects	SD	n
			Lower	Upper			
Intercept	**0.623**	**0.036**	**0.563**	**0.679**	Female ID (Intercept)	0.01	1203
KD490	-0.012	0.029	-0.059	0.034	Male ID (Intercept)	0.01	1316
Laying date	**-0.081**	**0.042**	**-0.149**	**-0.012**	Year (Intercept)	0.04	9
Establishment timing [a]							
During the survey	-0.007	0.046	-0.082	0.066			

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 Nests established prior to the initial survey were used as reference level.

Apéndice II.

Table S1. Time window model selection. Evaluation of the most probable time windows of SST and rainfall influencing hatching success, fledging success, and fledgling body condition. ΔAICc values are presented relative to the baseline model. If more than one model had the same ΔAICc values (or their difference was less than 2 AIC units) and their Pc values were < 0. 05, we considered them to be equivalent. When equivalent models were found, the most parsimonious one was selected (for example, a model with a linear expression of the SST was preferred over a model with a quadratic expression of the same weather variable).

Model	Weather condition	Statistic	Function	ΔAICc	Window opens	Window closes	Pc
a) Hatching success							
1	**SST**	**mean**	**quad**	**-148.97**	**9**	**1**	**0.006706348**
2	SST	min	quad	-141.76	5	1	0.003647285
3	SST	mean	lin	-138.91	5	2	0.003936183
4	SST	min	lin	-138.32	4	1	0.000733461
5	SST	max	quad	-135.7	5	3	0.002688201
6	SST	max	lin	-129.05	5	3	0.000995838
7	Rainfall	max	quad	-76.05	8	0	0.001835167
8	Rainfall	min	quad	-56.45	5	2	0.002137995
9	Rainfall	min	lin	-45.42	6	2	0.0014593
10	Rainfall	mean	quad	-42.99	7	0	0.00249067
11	Rainfall	max	lin	-26.42	10	3	0.001160327
12	Rainfall	mean	lin	-25.32	7	0	0.001351948
Model	Weather condition	Statistic	Function	ΔAICc	Window opens	Window closes	Pc
b) Fledging success							
1	**Rainfall**	**min**	**quad**	**-36.88**	**14**	**12**	**0.00277757**
2	SST	min	lin	-34.83	6	5	0.03398163

3	Rainfall	mean	quad	-34.23	18	6	0.00164545
4	Rainfall	max	quad	-33.91	18	13	0.00164545
5	Rainfall	min	lin	-33.46	14	12	0.00071761
6	SST	min	quad	-32.97	6	5	0.1296061
7	SST	mean	lin	-32.26	18	0	0.1155135
8	SST	max	lin	-31	6	6	0.07173641
9	SST	mean	quad	-30.88	16	0	0.1873688
10	Rainfall	max	lin	-30.76	10	7	0.00093268
11	SST	max	quad	-30.25	15	6	0.1223853
12	Rainfall	mean	lin	-23.62	10	7	0.00582313

Testing the SST window controlling by the rainfall window

1	SST	mean	lin	-1.89	15	15	0.8051243
2	SST	max	lin	-1.89	15	15	0.8184801
3	SST	min	lin	-2.2	19	15	0.8648162
4	SST	mean	quad	-2.74	2	2	0.8487342
5	SST	max	quad	-2.74	2	2	0.8648162
6	SST	min	quad	-3.21	20	15	0.9118836

Testing the SST window controlling by the rainfall window

1	Rainfall	mean	lin	-14.92	6	6	0.2516143
2	Rainfall	max	lin	-14.92	6	6	0.1229935
3	Rainfall	min	lin	-17.24	6	5	0.2404303
4	Rainfall	mean	quad	-12.92	6	6	0.3222849
5	Rainfall	max	quad	-12.92	6	6	0.1593759
6	Rainfall	min	quad	-15.47	6	5	0.2660718

c) Fledgling body condition

1	**SST**	**mean**	**quad**	**-89.14**	**19**	**1**	**0.01364904**
2	SST	mean	lin	-83.56	19	1	0.00517263
3	SST	min	lin	-83.23	14	9	0.00338851
4	SST	min	quad	-79.89	14	9	0.01962816
5	SST	max	quad	-73.22	12	12	0.00848839
6	SST	max	lin	-65.55	12	12	0.010008

7	Rainfall	min	quad	-17.9	6	2	0.7166401
8	Rainfall	mean	lin	-11.12	19	13	0.01892984
9	Rainfall	mean	quad	-9.32	16	13	0.1054614
10	Rainfall	max	quad	-8.85	16	13	0.09387233
11	Rainfall	min	lin	-5.8	12	3	0.7526031
12	Rainfall	max	lin	-4.2	20	13	0.1702439

Best supported climate windows are presented in bold. Both for sea surface temperature (SST) and rainfall, three statistics (mean, maximum, and minimum) along with their lineal and quadradic functions were tested. For all models, ΔAICc denote the difference in AICc scores between the current model and a null model (i.e., a model without a climate signal), and Pc values denote the probability that the climate signal is a false positive.

Apéndice III. Producción científica adicional durante el doctorado

Extra-pair offspring of the blue-footed booby show no sign of higher fitness in the first ten years of life.

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Animal Behaviour

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Abstract

According to the good genes and genetic compatibility hypotheses, females of socially monogamous species obtain genetic benefits for their offspring by performing extra-pair (EP) copulations with males of higher quality than their social mates or males with whom they are more genetically compatible. If EP offspring do receive genetic benefits in the form of advantageous alleles or more compatible allele combinations, they should outperform their within-pair (WP) half-siblings concerning survival and/or reproductive output. Here, we followed 52 EP and 737 WP blue-footed booby (*Sula nebouxii*) offspring during their first ten years of life (excluding the embryonic period and the first 10 days after hatching) to assess whether they differed in: fledging probability, fledgling body condition, recruitment probability, age at first reproduction, number of breeding events, and accumulated breeding success. EP and WP offspring did not differ in any of these proxies of fitness. Furthermore, we found that extra-pair offspring were equally likely to occur in any hatching position. However, differences in fledgling production over the lifetime could not be ruled out, and because only WP production of eggs and fledglings was tallied, the possibility remains that EP offspring could produce more EP offspring later in life than do WP offspring. Furthermore, the possibility of context-dependent genetic benefits occurring only under stressful conditions cannot be discounted because our sample of offspring was obtained in a single exceptionally favourable reproductive season.

Keywords: Blue-footed booby, extra-pair paternity, infidelity, genetic benefits, good genes, compatibility, hatching position

Long-term effects of sex-specific sibling interaction on the development of blue-footed boobies

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Behavioral Ecology and Sociobiology

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Abstract

The sex of an animal's siblings can potentially have long-term effects on its development if it competes or cooperates with them in a brood or litter. For the first test of lifelong developmental effects of infant siblings' sex in a wild animal, we monitored broods of two blue-footed booby (*Sula nebouxii*) chicks that recruited intact into their natal breeding population. Female chicks grow to be 27% heavier than male chicks and broodmates compete aggressively for food during 10 weeks. We took hatch order into account because first-hatched chicks aggressively dominate their siblings and sometimes kill them, and second-hatched chicks experience chronic stress. We confirmed only one of 20 predictions for long-term effects of sibling sex: females with elder brothers had lower odds of hatching their eggs than females with elder sisters. However, sex of their elder sibling made no difference to a female's or male's age of first reproduction, annual survival, fledging success, age of last sighting, or accumulated breeding success. Based on 760 recruits from 18 birth cohorts, these findings suggest that, although a sibling´s sex could, for all we know, affect an individual´s survival in the nestling or juvenile stages, long-term effects on survival and reproductive performance in the adult stage are mostly absent or inconsequential in two-chick broods that recruit intact. This resilience is likely due to evolved developmental buffering of adult survival and reproductive performance, but impacts of a sibling's sex on development and survival during the nestling and juvenile periods remain to be tested.

Keywords: Keywords: sex-specific sibling effects; lifelong developmental influence.

How removal of cats and rats from an island allowed a native predator to threaten a native bird

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Biological Invasions

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Abstract

The question of how to program the removal of two invasive mammals, typically cats and rats, from a marine island without increasing risk to native prey species has received two general answers based on ecological theory: removal of cats must be accompanied by control of their mesopredator prey, and risk is minimized by removing both invaders simultaneously. Nonetheless, a 31-year study showed that in a 82-ha tropical marine bird sanctuary, predation on a native prey, the blue-footed booby, by a native predator, the Atlantic Central American milk snake, apparently diminished after removal of cats then increased elevenfold after the additional removal of black rats. These novel effects are explained in terms of a hypothetical three-link trophic web in which cat removal released rats to increasingly compete with or prey on the snakes that feed on hatchling boobies, and subsequent rat removal released snakes from all remaining predation. The upshot is a disturbing scenario in which approximately 200 milk snakes currently aggregate annually in roughly 1 hectare of booby colony and predate roughly forty percent of the hatchlings. Where the lowest link of an insular trophic web is a native mesopredator that feeds on native prey, the predictions of the classic mesopredator release scenario can be inverted, and removal of invasive mammals may endanger native prey species.

Keywords

island, mesopredator release, invasive mammals, marine bird, snake predation