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Body size variation in a tropical seabird along a latitude-productivity gradient

Alberto Piña-Ortiz[1] · José Alfredo Castillo-Guerrero[2] · Luis Manuel Enríquez-Paredes[3] · Guillermo Fernández[4] · Salvador Hernández-Vázquez[2] · Petra Quillfeldt[1]

Abstract

Body size can vary across geographical gradients, and these clines have been mainly attributed to temperature (i.e., the heat conservation hypothesis). However, in tropical areas, this pattern is not necessarily fulfilled. Furthermore, it is not known whether a body size cline is sex-biased in dimorphic species. Therefore, we aimed to evaluate the intra-specific variation in body size in a tropical seabird, the Red-billed Tropicbird (*Phaethon aethereus*), at six breeding colonies in the Pacific Ocean (17–31° N) and to relate body traits to environmental variables in each colony. Further, we examined sexual size dimorphism (SSD) in the species and its possible influence on the pattern of inter-colony variation in body size. We measured body traits in 187 adults. SSD was evaluated using culmen, ulna, and tarsus lengths and body mass. Chlorophyll-a, air temperature, and sea surface temperature (SST) values within an 80-km radius of each breeding site and the latitude of each island were used to create an environmental index. The relationships between body traits and the environmental index were assessed using regression models. Red-billed tropicbirds exhibited a positive, south-to-north body-size cline (between 1 and 9%) related to environmental conditions, and SSD was evident at only two northern colonies (males > females). The body size cline in the species could be influenced by a set of abiotic and biotic factors, which has likely led to phenotypic plasticity. The sexual dimorphism detected in colonies with larger body sizes along with high chlorophyll-a values and low SST values suggest that environmental-mediated variation in body size is a crucial mediator of SSD.

Keywords Body-size cline · Local environmental conditions · *Phaethon aethereus* · Phenotypic plasticity · Sexual size dimorphism

✉ José Alfredo Castillo-Guerrero
alfredo.castillo@academicos.udg.mx

1   Department of Animal Ecology and Systematics, Justus
    Liebig University (JLU) Giessen, Heinrich-Buff-Ring 26,
    35392 Giessen, Germany

2   Departamento de Estudios para el Desarrollo Sustentable
    de la Zona Costera, Centro Universitario de la Costa
    Sur, Universidad de Guadalajara, Gómez Farías
    82, San Patricio-Melaque, Municipio de Cihuatlán,
    Jalisco C.P. 48980, México

3   Facultad de Ciencias Marinas, Universidad Autónoma
    de Baja California, Carretera Transpeninsular
    Ensenada-Tijuana 3917, Colonia Playitas, Ensenada,
    Baja California C.P. 22860, México

4   Unidad Académica Mazatlán, Instituto de Ciencias del
    Mar y Limnología, Universidad Nacional Autónoma
    de México, Av. Joel Montes Camarena S/N, Mazatlán,
    Sinaloa C.P. 82040, México

Zusammenfassung

Variation der Körpergröße bei einem tropischen Seevogel entlang eines Breitengrad-Produktivitäts-Gradienten.

Die Körpergröße von Tieren kann über geografische Gradienten hinweg variieren, und diese Unterschiede wurden hauptsächlich auf die Temperatur zurückgeführt (Hypothese der Wärmeerhaltung). In tropischen Gebieten trifft dieses Muster jedoch nicht unbedingt zu. Darüber hinaus ist nicht bekannt, ob die Körpergröße bei dimorphen Arten geschlechtsabhängig ist. Aus diesem Grund haben wir uns zum Ziel gesetzt, bei einem tropischen Seevogel, dem Rotschnabel-Tropikvogel (*Phaethon aethereus*), in sechs Brutkolonien im Pazifischen Ozean (17–31° N) die intra-spezifische Variation der Körpergröße zu untersuchen und Körpermerkmale mit Umweltvariablen in der Kolonie in Beziehung zu setzen. Darüber hinaus untersuchten wir den sexuellen Größendimorphismus (SSD) bei dieser Art und seinen möglichen Einfluss auf die Variation der Körpergröße zwischen den Kolonien. Wir haben die Körpermerkmale von 187 erwachsenen Tieren gemessen. Die SSD wurde anhand der Länge von Schnabellänge, Ulna und Tarsus sowie der Körpermasse bewertet. Chlorophyll-a, Lufttemperatur und Meeresoberflächentemperatur (SST) in einem 80-km-Radius um jeden Brutplatz sowie der Breitengrad jeder Insel wurden zur Erstellung eines Umweltindex verwendet. Die Beziehungen zwischen den Körpermerkmalen und dem Umweltindex wurden mithilfe von Regressionsmodellen bewertet. Rotschnabel-Tropikvögel von Süden nach Norden verlaufende Zunahme der Körpergröße (zwischen 1–9%) auf, die mit den Umweltbedingungen zusammenhing. SSD (Männchen > Weibchen) war nur in zwei nördlichen Kolonien zu beobachten. Das Körpergrößengefälle bei dieser Art könnte durch eine Reihe von abiotischen und biotischen Faktoren beeinflusst werden, die zu phänotypischer Plastizität führen. Der sexuelle Dimorphismus, der in Kolonien mit größeren Körpergrößen zusammen mit hohen Chlorophyll-a-Werten und niedrigen SST-Werten festgestellt wurde, legt nahe, dass umweltbedingte Variationen der Körpergröße ein entscheidender Vermittler von SSD sind.

Introduction

Physical traits in terrestrial and aquatic vertebrates (e.g., fish, mammals, and birds) often show substantial variation across geographical gradients (Ashton 2002; Rodríguez et al. 2006; Emmrich et al. 2014; Bandeira et al. 2016). These geographical body-size clines have been attributed to abiotic (e.g., sea surface temperature, air temperature, latitude, longitude, and wind speed) and biotic factors (e.g., competition, predation, genetic differentiation, sexual selection, and prey availability). However, the influence of abiotic factors has been investigated with greater intensity (Jakubas et al. 2014; Bandeira et al. 2016; Seeholzer and Brumfield 2017). Research on geographical body size variation in multiple animal taxa has focused on Bergmann's rule at interspecific scales (Bergmann 1847) or James' rule (proposed by Blackburn et al. 1999) at intraspecific scales (Rensch 1938; James 1970). These rules assume that heat loss from an endothermic organism is proportional to its surface area:volume ratio (heat conservation hypothesis). Hence, species distributed along a latitudinal gradient are expected to show a geographical body-size cline, with small and large body sizes in warmer and colder areas, respectively (Bergmann 1847; Blackburn et al. 1999).

Intraspecific variation in seabird body size along large-scale climatic gradients has been evaluated over extensive distribution ranges or even the entire distribution ranges of species that inhabit temperate or polar regions, and the resulting body size clines have been found to follow either the rules of Bergmann or James (Moen 1991; Barrett et al. 1997; Wojczulanis-Jakubas et al. 2011; Jakubas et al. 2014;

Yamamoto et al. 2016). However, when evaluating the body-size clines of seabirds distributed in tropical regions, the resulting patterns have not entirely fit the established assumptions of either rule (Le Corre and Jouventin 1999; Nunes et al. 2017). Furthermore, no direct relationship between body size and air temperature has been found in tropical areas, suggesting that temperature is only a key determinant of body size below a certain threshold (Geist 1987; Rodríguez et al. 2006). Thus, it has been suggested that while temperature plays a vital role in determining variations in body size in temperate and cold areas, other environmental (e.g., chlorophyll-a and wind speed), genetic (e.g., population structure), and/or ecological (e.g., foraging behavior) factors may also influence this trait among populations distributed over large tropical and subtropical areas (Jakubas et al. 2014; Yamamoto et al. 2016; Nunes et al. 2017).

Seasonal and large-scale marine primary productivity is not necessarily directly related to latitude (Longhurst et al. 1995; Ma et al. 2014), although small-scale marine provinces show latitudinal gradients in primary productivity (e.g., Gulf of California and Mexican Tropical Pacific; Wilkinson et al. 2009). Thus, primary productivity values around seabird colonies could result in local divergences in body size among neighboring populations due to the different environmental pressures that each population might face at each site (Barbraud et al. 1999; Friesen 2015; Nunes et al. 2017).

Populations subject to different environmental conditions are also subject to different selective pressures, and thus local adaptation can act as a barrier to gene flow

among wild populations under these circumstances (Sexton et al. 2014). Individuals that remain within population-specific non-breeding grounds or near the colony boundaries throughout the year could avoid exposure to atypical environmental conditions, which would in turn result in the positive selection of individuals that are best suited to the local conditions, with the resulting diversity due to phenotype and genotype shaping (Friesen 2015). Hence, it is reasonable that body size traits can be shaped by environmental variables operating on both large (e.g., air temperature) and small (e.g., local levels of phytoplankton biomass or chlorophyll-a) scales, with larger and heavier individuals occurring in productive and high-latitude areas (Nunes et al. 2017).

In addition to the geographical variation in body size, sexual size dimorphism (SSD) is relatively common in seabirds (Fairbairn and Shine 1993; Serrano-Meneses and Székely 2006; Manciniet al. 2013), with sexual selection notably influencing seabird SSD (Barbraud and Jouventin 1998; Serrano-Meneses and Székely 2006; Dale et al. 2007). Multiple abiotic factors have been proposed to explain the variation in SSD in vertebrate and invertebrate taxa (Blanckenhorn et al. 2006; Roitberg 2007; Stillwell and Fox 2007; Lengkeek et al. 2008; Ulian and Rossi 2016). For instance, temperature may help drive selection by affecting males and females differently, with substantial differences in the extent of SSD among populations within a given range (Blanckenhorn et al. 2006; Stillwell and Fox 2007). Furthermore, comparative analyses of SSD within and across species have found a greater extent of SSD at the intraspecific level than at the interspecific level (Ulian and Rossi 2016). In addition, some studies have shown that male body size within a given species varies with latitude to a greater extent than female body size. Thus, some factor that varies systematically with latitude is responsible for producing this pattern (Blanckenhorn et al. 2006). However, in seabirds, the question of whether adults of sexually dimorphic species exhibit similar or sex-biased geographical variation patterns in body size has never been evaluated, even though body size variation has been observed in both males and females of sexually dimorphic seabird species (Jakubas et al. 2014; Yamamoto et al. 2016; Nunes et al. 2017).

The Red-billed Tropicbird (*Phaethon aethereus*) is a pelagic seabird with a pantropical oceanic distribution (Orta et al. 2020). This medium-sized (550–750 g) long-lived seabird breeds annually, laying a single egg inside crevices or caves, and becomes a central-place forager during the breeding season, conducting foraging trips of up to 600 km from its breeding sites (Nelson 2006; Diop et al. 2018). Parental care is shared between pair members, with the incubation and fledgling stages lasting approximately 43 and 85 days, respectively (Castillo-Guerrero et al. 2011). In the Atlantic Ocean, a slight male-biased SSD has been reported (SSD

index of 1.01–1.03 for all significant body traits; Nunes et al. 2013).

Red-billed Tropicbird breeding colonies in the Pacific Ocean are distributed from the Gulf of California and Revillagigedo Archipelago in Mexico to Chañaral Island in Chile and the Galapagos Islands (Nelson 2006). Red-billed tropicbirds breed on a total of 14 islands along the Mexican Pacific, including those of the Gulf of California and the Mexican Tropical Pacific, where latitudinal gradients in primary productivity (north-to-south) and sea surface temperature (SST; south-to-north) are present (Wilkinson et al. 2009; Piña-Ortiz et al. 2018). In addition, low genetic differentiation and a high degree of connectivity between populations have been reported for the species in this region (Castillo-Guerrero et al. 2020).

This study aimed to evaluate the variation in body size between breeding red-billed tropicbirds across their distribution range in the Mexican Pacific (18–31° N, 104–114° W) by examining the relationships between body traits and the environmental variables (i.e., air temperature, SST, and chlorophyll-a) that characterize each breeding area. We weighed and measured the body traits of red-billed tropicbirds at six breeding colonies found on the islands in the study area. As males are larger than females (Nunes et al. 2013), we also evaluated if sexual dimorphism influenced any patterns of inter-colony variation in body size. We predicted that males would be larger than females and that a positive relationship between SSD and body size would be present. Thus, SSD would be greater in colonies where larger individuals were present compared to the SSD values of colonies composed of smaller individuals. We also predicted that a latitudinal south-to-north increase in body size would be present that reflected the variability in local environmental conditions given that individuals breeding at higher latitudes utilize oceanic areas with higher chlorophyll-a and lower air temperature and SST values than those breeding at lower latitudes.

Materials and methods

Study area and fieldwork

We collected body size data in six colonies during the breeding season in the incubation and chick-rearing stages from October to May 2012–2013, 2015–2016, and 2020–2021 (Table 1). The study colonies were located on islands across the breeding range of the Red-billed Tropicbird in the Mexican Pacific from 17–31° N. From north to south, the study colonies were San Jorge (SNJ), which is one of the northernmost colonies for the species; San Pedro Mártir (SPM); Farallón de San Ignacio (FSI); Isabel (ISA); Peña Blanca (PBL); and Morros El Potosí (MEP; Fig. 1). The selected colonies

Table 1 Sampling dates, location, island area and number of breeding pairs in six colonies of the red-billed tropicbird (*Phaethon aethereus*) sampled throughout the Gulf of California and Mexican Tropical Pacific between 2012 and 2021

Study island[a] and sample size (*n*)	Population size[b] (breeding pairs)	Geographic location	Island area (ha)	Sampling collection dates
SNJ (23)	5–17	31° 00′ 45′′N, 113° 14′ 38′′W	14	Feb 2015
SPM (43)	150–190	28° 22′ 52″N, 112° 18′ 23″W	267	May 2012, Jan 2015, Feb 2020
FSI (20)	150–228	25° 26′ 15′′N, 109° 22′ 39′′W	17	Mar 2012, May 2013
ISA (11)	87–155	21° 50′ 40′′N, 105° 53′ 02′′W	194	Apr 2015
PBL (68)	1,200–1,650	19° 06′ 11′′N, 104° 29′ 12′′W	10	Oct–Dec 2015, Feb 2016, Feb-Mar 2020
MEP (22)	100	17° 31′ 57′′ N, 101° 29′ 18′′ W	15	Jan 2021

[a]Study islands: *SNJ* San Jorge; *SPM* San Pedro Mártir; *FSI* Farallón de San Ignacio; *ISA* Isabel; *PBL* Peña Blanca; *MEP* Morros El Potosí

[b]Population sizes were reviewed in Piña-Ortiz et al. 2018. For details of the original source, see publication
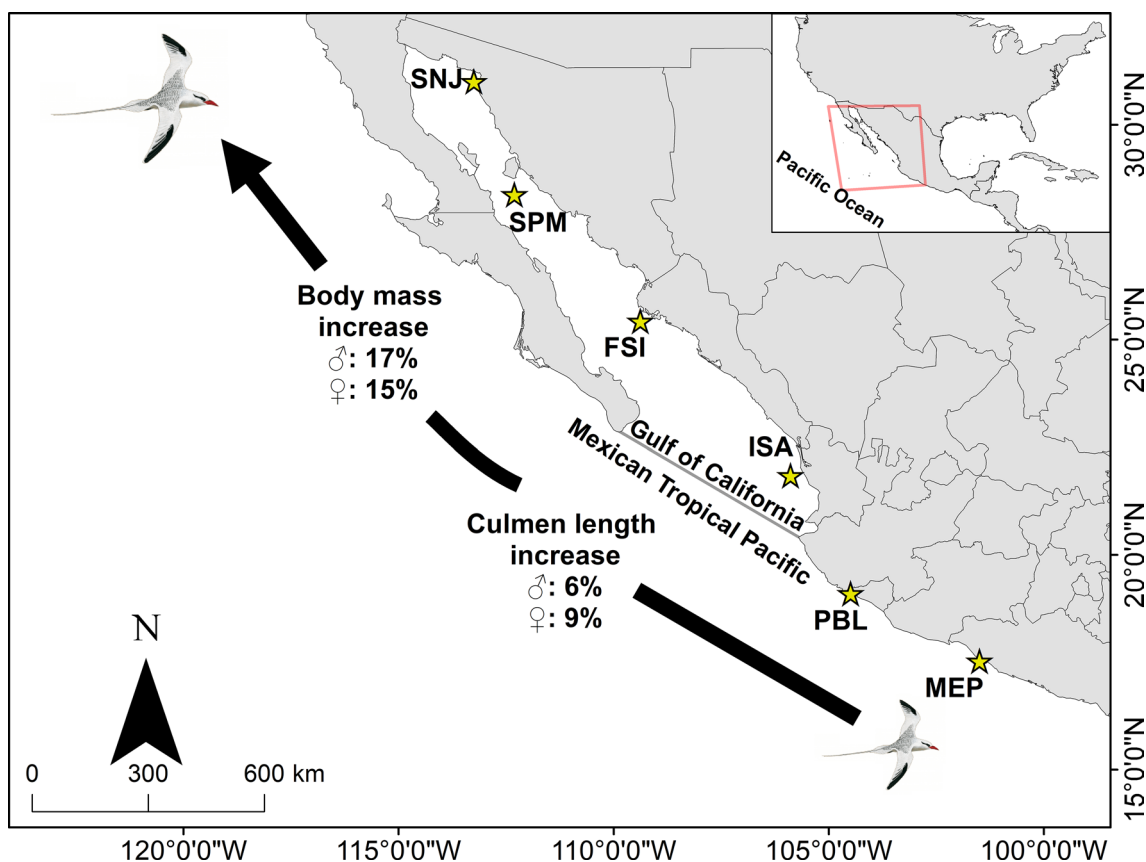

Fig. 1 Geographic locations of red-billed tropicbird colonies in the Gulf of California and Mexican Tropical Pacific sampled in this study. The solid line shows the boundary between the two ecological regions where the breeding sites are distributed. Black arrows indicate the clinal increase in body mass and culmen length (%) shown by males (♂) and females (♀) from south to north. Study locations from north to south: *SNJ* = San Jorge; *SPM* = San Pedro Mártir; *FSI* = Farallón de San Ignacio; *ISA* = Isabel; *PBL* = Peña Blanca; *MEP* = Morros El Potosí

varied in population size from a few pairs in SNJ to 1600 breeding pairs in PBL (Piña-Ortiz et al. 2018; Table 1). The distances between neighboring islands ranged from ~ 300 km (SNJ to SPM) to ~ 550 km (FSI to ISA). Four study colonies were found on islands in the Gulf of California, while the

other two were found on islands in the Mexican Tropical Pacific (Wilkinson et al. 2009; Fig. 1).

The Gulf of California is a mainly subtropical system, although the northern Gulf of California resembles a temperate system during winter and has exceptionally high rates of

primary productivity due to its topography, warm climate, and upwelling systems (Lluch-Cota et al. 2007). This high primary productivity supports large populations of small pelagic fish, which constitute the primary food source for many piscivorous animals, including squid, fish, seabirds, and marine mammals (e.g., the California sea lion [*Zalophus californianus*]; Mercado-Santana et al. 2017). Upwelling generally occurs off the mainland coast with northwesterly winds during winter (December–May) and on the Baja California coast with southeasterly winds during summer (July–October). June and November constitute transition periods (Lluch-Cota et al. 2007). The Mexican Tropical Pacific is a highly productive region influenced by the southernmost portion of the California Current during the winter, which seasonally transforms the conditions of this region from tropical to subtropical. The northernmost limit of the Mexican Tropical Pacific extends to the area where the California Current turns westward during summer, leaving behind a region under the influence of the warm Costa Rica Coastal Current. This complex region also includes a narrow shelf that steeply drops off to great oceanic depths (Wilkinson et al. 2009).

In general, latitudinal gradients of primary productivity and SST throughout the year have been documented for both regions, with the highest and lowest values of primary productivity observed in the north and south, respectively, and SST showing the opposite pattern (Pennington et al. 2006; Lluch-Cota et al. 2007). However, this observed gradient is not related per se to latitude but is influenced by topography, sea currents, and upwellings. In the Gulf of California, for example, it has been pointed out that the northernmost regions maintain high levels of productivity throughout the year because of strong tidal currents that lead to constant water-column mixing (Simpson et al. 1994). In the Midriff Islands region, strong tidal mixing influences water-column conditions up to 500 m depth and brings nutrient-rich waters toward the surface and subsurface layers, creating conditions of constant upwelling (Álvarez-Borrego 2002). In contrast, the southern region is the deepest within the Gulf of California and has been described as complex given that its thermohaline structure is related to the mixing of the North Equatorial Current, California Current, and the waters of the Gulf of California, which is reflected in the relatively low productivity values observed in this portion of the gulf (Álvarez-Borrego 2012; Lavín et al. 2013; Mercado-Santana et al. 2017).

We hand-captured 187 breeding adults in nest burrows during incubation or chick-rearing stages and measured their body mass and culmen, ulna, and tarsus lengths (Figure S1, Table S1). We measured body mass using a portable electronic scale to the nearest 5 g, and the remaining measurements were taken using vernier calipers (±0.01 mm; Table S1). To avoid resampling, we marked the measured birds with alphanumeric bands on the tarsus or non-toxic paint on the culmen. Measurements were collected for both adults if both were in the nest, and measurements were only taken once per nest. A. Piña-Ortiz and J. A. Castillo-Guerrero collected the measurements. They measured the same 22 individuals (4 in SPM and 18 in PBL) included in this study. Pearson correlation tests were performed for ulna, culmen, and tarsus lengths to evaluate the relationships among the body traits measured by both authors. All body lengths collected by both researchers were significantly correlated with each other ($r = 0.63$–0.77; p values < 0.002 for all pairwise comparisons).

Sex determination

We took a blood sample of each specimen from the brachial vein with a 16-mm 25G needle and stored the sample in a buffer (100 mM tetrasodium EDTA, 100 mM Tris, 10 mM NaCl, and 1% sodium dodecyl sulfate). Afterward, we extracted the genomic DNA from the blood samples in the laboratory following a proteinase K and salt-extraction protocol (Aljanabi and Martinez 1997). DNA quantification and quality were assessed by electrophoresis on 1.5% agarose gels stained with ethidium bromide (0.5 µg/ml). A 1000-bp molecular weight marker (DNA size standard Invitrogen™) was used to determine the relative concentration of the extracted genetic material. This process allowed us to identify low-yielding samples likely to result in low amplification (allelic dropout or shorter fragment dominance). These samples were re-extracted or re-precipitated to obtain a concentration between 15 and 25 ng/µl. Molecular sexing was performed using 2550/2718 primers (Fridolfsson and Ellegren 1999). The Polymerase Chain Reactions (PCR) contained 1xPCR buffer (20 mM Tris–HCl, 50 mM KCl, 1.5 mM $MgCl_2$, and 0.2 mM dNTPs), 0.7 µM of each primer, 0.8 U of Taq DNA polymerase (Invitrogen, Waltham, USA), and 15–25 ng of template DNA in a total volume of 25 µl. Thermal cycling consisted of 4 min at 94 °C followed by 30 cycles of 30 s at 94 °C, 30 s at 52 °C, and 30 s at 72 °C, with a final extension of 5 min at 70 °C. We separated the PCR products by electrophoresis in 2.0% agarose gels stained with ethidium bromide (0.5 µg/ml). The direct observation of gels under UV transillumination revealed that individuals identified as males were characterized by only one band on the gel, while two bands characterized females (Fig. S2).

Blind sample replicates (15%) and positive and negative controls were systematically performed for each set of amplifications to avoid incorrect assignments or false positives. Samples from known blue-footed booby (*Sula nebouxii*) female and male specimens were used as positive controls. Negative controls included two no template reactions: one from a no-tissue sample extraction and another using ultrapure water. Of the 187 individuals, 171 birds

were successfully sexed (91.44%). However, samples from 3 individuals (1.66%), 1 individual (0.55%), 12 individuals (6.6%), and 1 (0.55%) individual in SPM, FSI, PBL, and MEP, respectively, failed to amplify, and thus their sex could not be confirmed. This result may have been due to the low amounts of DNA in these samples.

Environmental data

For the study area, we obtained environmental data of SST (°C; 11 μm SST algorithm) and chlorophyll-a concentrations (mg/m³; chlorophyll OCx algorithm) between August 2002 and January 2021 from the Aqua-Modis Sensor (NASA/GSFC-OBPG 2014). First, we downloaded a monthly data series of each oceanographic variable with 4 km per pixel resolution. Then, the year-round average SST and chlorophyll-a values were calculated within an 80-km radius surrounding each colony, according to the average foraging distance used by breeding red-billed tropicbirds from Peña Blanca Island to feed their chicks (González-Zamora 2019). Likewise, air temperature data for each study island was obtained from the nearest weather station (Puerto Peñasco station 26072 for SNJ, Bahía de Kino station 26179 for SPM, Topolobampo [DGE] station 25098 for FSI, San Blas station 18029 for ISA, Manzanillo [OBS] station 6018 for PBL, and Zihuatanejo [DGE] station 12127 for MEP; data available from www.smn.conagua.gob.mx/es/climatologia/informacion-climatologica/informacion-estadistica-climatologica). We used the average monthly air temperature data available between January 1975 and December 2015 recorded by each weather station.

Statistical analyses

We used culmen, ulna, and tarsus lengths and body mass data to perform range-wide statistical analyses (Table S1). First, we plotted the data set for each variable per island to look for outliers and identify possible sampling errors in morphometric measurements. To identify outliers, we employed the criterion of Nunes et al. (2017), which considers data outside ± 2 standard deviations from the mean as outliers. Next, we used Pearson correlation tests with Bonferroni correction for multiple testing ($\alpha = 0.012$, for 4 comparisons). Finally, to evaluate the relationships between morphometric variables and body mass, all morphometric variables were positively correlated among themselves and with body mass ($r = 0.21$–0.55; p-values 0.007 to < 0.001 for all pairwise comparisons; Fig. S3), except the correlation between ulna and tarsus lengths ($r = 0.18$; $p = 0.021$).

Subsequently, we employed a principal component analysis (PCA) to create a composite body size index for each individual. This index was obtained by incorporating all body measurements (culmen, ulna, and tarsus lengths) except body mass, as it could vary depending on the time of capture (i.e., breeding stage or before or after feeding a chick). However, as the first principal component (PC1) only explained 51.8% of the variance in body measurements, we did not consider it useful as an integrative measure of body size. Therefore, we used each body trait and mass independently in subsequent analyses.

We compared body size measurements between sexes and breeding populations using a two-way MANOVA with Wilk's lambda (λ) and a post hoc Fisher least significant difference test. Likewise, univariate normality was evaluated with the Shapiro–Wilk test using the residual values of each body measurement, and multivariate normality was evaluated with the Mardia test of skewness and kurtosis, Henze–Zirkler test, and Royston test with the R package MVN (Korkmaz et al. 2014). Considering the possible variations in the body mass of individuals at the time of capture, we used a general linear model (GLM) where colony, sex, and breeding stage were considered as categorical variables and the date of collection as a covariate. The GLM showed that date ($F_{1,137} = 11.87$, $p < 0.001$) significantly influenced the final model selected. Therefore, we standardized the body mass of all individuals using the adjusted means (covariate = day 52) in the subsequent analyses where this variable was analyzed.

We used regression models to explain the relationships between morphometric structures and body mass, and environmental variables. Prior to conducting regression modelling, correlations between environmental variables (i.e., air temperature, SST, and chlorophyll-a) and latitude (in decimal degrees) were analyzed with Pearson correlation tests with Bonferroni correction for multiple testing ($\alpha = 0.012$). All variables were highly correlated ($r = -0.87$ to 0.95, p-values < 0.001; Fig. S4). Thus, we used a PCA to create an environmental index (PC1: 96.8% of the total variance) to avoid redundancy and multicollinearity between variables. The regression models were run with the environmental index as an explanatory variable and the means of body structures (culmen, ulna, and tarsus lengths), and the adjusted mean of body mass as response variables. We analyzed each explanatory variable in independent models considering the male and female datasets separately. The assumptions of all parametric tests used in this study were assessed and fulfilled by the data. All statistical analyses were carried out in STATISTICA 7.1 (Hill and Lewicki 2007) except for the univariate and multivariate normality tests used for the MANOVA analyses, which we performed in R 3.6.2 (R Core Team 2020). Body traits and mass are reported as the mean $\pm$ standard deviation.

Results

After removing outliers, all body traits showed a multivariate normal distribution for all breeding islands. In addition, a global difference was found for body traits (Wilk's $\lambda = 0.33$, $F_{20,20} = 9.14$, $p < 0.001$) and body mass ($F_{5,137} = 17.41$, $p < 0.001$) among the individuals from the different breeding islands. Overall, both size and body mass increased to the north in females and males (between 1 and 9%; Table 2). However, no multivariate global differences between sexes were detected in body traits (Wilk's $\lambda = 0.96$, $F_{4,20} = 1.48$, $p = 0.21$) or body mass ($F_{5,137} = 17.41$, $p < 0.001$). Nevertheless, the post hoc test revealed a significant difference between sexes in the northern colonies of SPM (Fisher LSD test $p = 0.037$) and FSI (Fisher LSD test $p = 0.006$), with males showing larger culmens than those of females. Likewise, males from SPM had longer ulna lengths than females (Fisher LSD test $p = 0.027$; Table 2, Fig. 2).

All body traits and body mass were positively related to the environmental index for both females (culmen: $y = 2.21x + 61.15$, $R^2 = 0.45$, $p < 0.001$; ulna: $y = 1.08x + 103.30$, $R^2 = 0.17$, $p = 0.002$; tarsus: $y = 0.37x + 27.48$, $R^2 = 0.07$, $p = 0.017$; body mass: $y = 46.54x + 580.64$, $R^2 = 0.42$, $p < 0.001$) and males (culmen: $y = 2.22x + 62.03$, $R^2 = 0.46$, $p < 0.001$; ulna: $y = 1.70x + 102.91$, $R^2 = 0.38$, $p < 0.001$; tarsus: $y = 0.56x + 27.73$, $R^2 = 0.19$, $p < 0.001$; body mass: $y = 47.26x + 584.79$, $R^2 = 0.50$, $p < 0.001$; see Fig. 3).

Discussion

Geographical body size variation

Our results describe geographical variation in the body size of red-billed tropicbirds among six breeding colonies distributed throughout the Mexican Pacific. The body traits considered in this study increased from the south to the north and were related to local environmental conditions (i.e., air temperature, SST, and chlorophyll-a). These results agree with those found in other seabird species, such as the European storm petrel (*Hydrobates pelagicus*; Jakubas et al. 2014), streaked shearwater (*Calonectris leucomelas*; Yamamoto et al. 2016), and brown booby (*Sula leucogaster*; Nunes et al. 2017). Studies on seabirds distributed in temperate regions (e.g., European storm petrel and streaked shearwater) have generally found that body size variation conforms to the heat conservation hypothesis (i.e., Bergmann's rule). However, in tropical seabirds, it has been suggested that air temperature is not the only factor involved in shaping phenotypes, and other local oceanographic features may influence this process (Nunes et al. 2017). In our study, the high correlations among environmental variables preclude the identification of the contributions of different factors to variations in body size. However, as other studies have proposed, local oceanographic features, such as chlorophyll-a or ocean temperatures (SST), may be fundamental driving forces behind the geographical body size divergence in seabirds (Moen 1991; Barrett et al. 1997; Nunes et al. 2017). Thus, individuals belonging to northern colonies in the Gulf of California, where primary productivity (annual mean of 2.14 g C m^{-2} d^{-1}) values are high and SST (annual mean of 23.24 °C) is low, were the ones that showed larger body sizes compared to those in the southern Gulf of California (from the mouth to the central region; primary productivity of 0.92–1.52 g C m^{-2} d^{-1} and SST of 24.6–25.6 °C) and Mexican Tropical Pacific (0.82 g C m^{-2} d^{-1} and mean SST of 28 °C) where individuals were smaller (Wilkinson et al. 2009; Escalante et al. 2013).

Intraspecific body size variation among populations may reflect phenotypic plasticity or genetic differences as responses to local environmental conditions (local adaptation). It has been challenging to differentiate between genetic and environmental contributions to phenotypic variations in size. Some studies have established adaptive conclusions

Table 2 Mean ± standard deviation of ulna length, culmen length, tarsus length, and body mass measurements of the red-billed tropicbird (*Phaethon aethereus*) sampled from six colonies on Mexican islands

Breeding island[a] and sample size by sex (*n*)[b]	Ulna length (mm)		Culmen length (mm)		Tarsus length (mm)		Body mass (g)	
	Male	Female	Male	Female	Male	Female	Male	Female
SNJ (M = 12; F = 11)	104.37 ± 1.78	105.02 ± 1.16	63.20 ± 3.24	64.41 ± 2.41	28.05 ± 0.68	27.84 ± 0.88	646.67 ± 22.50	636.82 ± 47.61
SPM (M = 28; F = 12)	104.97 ± 2.56	103.54 ± 2.80	64.92 ± 1.82	63.01 ± 2.65	28.57 ± 0.85	28.07 ± 1.28	621.39 ± 57.76	624.90 ± 46.47
FSI (M = 10; F = 9)	104.23 ± 1.62	103.91 ± 1.56	64.77 ± 2.57	61.84 ± 2.82	27.74 ± 0.85	27.37 ± 0.70	611.20 ± 38.00	571.78 ± 46.81
ISA (M = 4; F = 7)	102.48 ± 1.25	103.79 ± 1.80	61.53 ± 2.09	60.77 ± 2.69	27.70 ± 0.80	27.03 ± 0.44	556.25 ± 13.77	579.29 ± 46.85
PBL (M = 29; F = 27)	101.81 ± 2.10	102.36 ± 3.24	59.92 ± 2.26	59.01 ± 1.75	27.11 ± 1.57	27.42 ± 1.72	548.28 ± 48.85	546.35 ± 46.47
MEP (M = 15; F = 6)	99.91 ± 1.78	100.88 ± 2.37	59.12 ± 1.71	58.70 ± 0.97	27.33 ± 1.17	27.17 ± 1.09	538.33 ± 51.05	540.0 ± 51.67

[a]Breeding islands: *SNJ* San Jorge; *SPM* San Pedro Mártir; *FSI* Farallón de San Ignacio; *ISA* Isabel; *PBL* Peña Blanca; *MEP* Morros El Potosí

[b] *M* Male; *F* Female

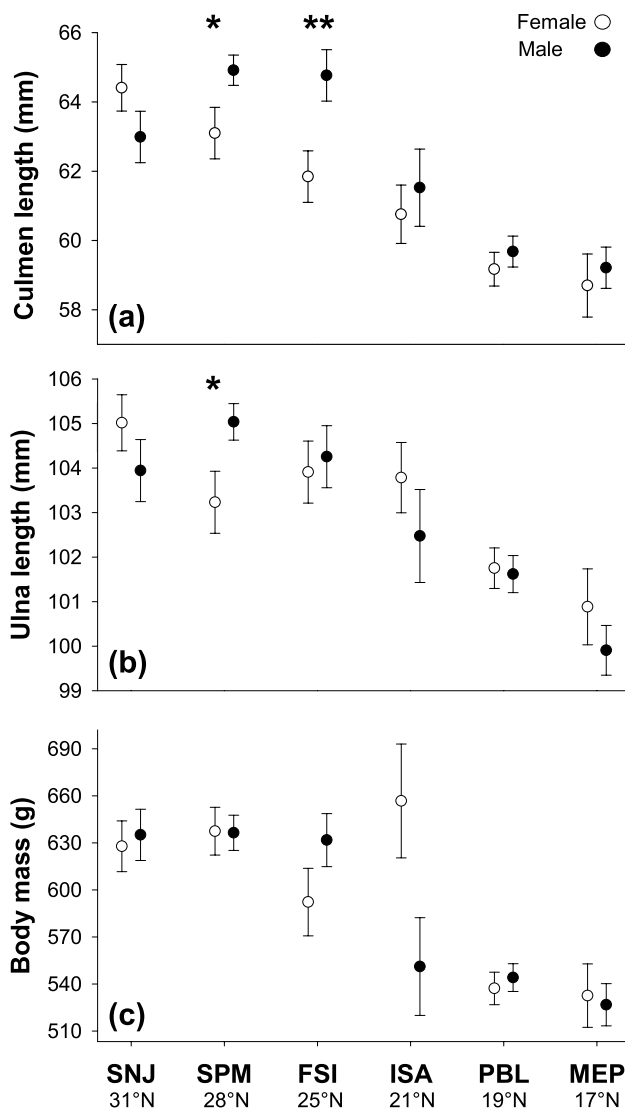**Fig. 2** Least square means ± standard error of **a** culmen length **b**, ulna length (both in mm), and **c** adjusted means ± standard error of body mass (*g*) of females and males of the red-billed tropicbird (*Phaethon aethereus*) distributed along a latitudinal gradient (north to south) in the Gulf of California and Mexican Tropical Pacific. Light and dark symbols, respectively, represent females and males. Adjusted means of body mass at day 52 are shown. *SNJ* = San Jorge; *SPM* = San Pedro Mártir; *FSI* = Farallón de San Ignacio; *ISA* = Isabel; *PBL* = Peña Blanca; *MEP* = Morros El Potosí. *Differences for $p < 0.05$; **differences for $p < 0.01$

based only on phenotypic measures of size (Stillwell 2010) without discerning whether the differences are related to local adaptation or phenotypic plasticity (Jakubas et al. 2014; Yamamoto et al. 2016). Other studies have determined long-term phenotypic changes in body size without evidence of genetic changes or differences in genetic structure (Moen 1991; Teplitsky et al. 2008; Husby et al. 2011). Few studies have attempted to assess the influence of both components in seabirds, for example, in the snow petrel (*Pagodroma*

nivea) although body size seems to be partly genetically determined, the relationship between adult size and food supply suggests that chick size may be influenced by food availability (Barbraud et al. 1999). In the study area, red-billed tropicbirds show low levels of genetic structure among colonies based on neutral markers (Castillo-Guerrero et al. 2020). Therefore, subject to certain caveats, we consider that body size variation could be primarily driven by phenotypic plasticity shaped by local oceanographic variables, with population genetic differentiation playing a secondary role.

Within this conceptual framework, local environmental conditions can promote different food availability scenarios among colonies and contribute to the inter-colony variation in body size. For example, the foraging strategies used by seabirds in a specific colony are subject to the resources available in the area (Botha and Pistorius 2018; Clay et al. 2019; Geary et al. 2019). Preliminary studies on the foraging ecology of the Red-billed Tropicbird indicate that the duration and distance of foraging trips vary between individuals from breeding colonies located in the Gulf of California and the Mexican Tropical Pacific, with breeding individuals from the southern colonies (e.g., PBL) making longer and more distant trips compared to those in northern colonies (e.g., SPM; Piña-Ortiz et al. unpubl. data). This result is consistent with the higher productivity registered for the Gulf of California compared to that of the tropical Pacific. In addition, the resources provided to offspring during the chick growth stage are crucial for determining the body size of adult seabirds (Barbraud et al. 1999; Quillfeldt and Peter 2000). Thus, it would be expected that food availability would be low in areas or times of low productivity compared to that in areas or times of high primary productivity, which in turn would be reflected in chick growth rates that depend on the number of feeding events and the nutritional quality of the prey (Barbraud et al. 1999; Quillfeldt et al. 2007; Grissot et al. 2019; Ausems et al. 2020). Under this scenario, food availability controlled by oceanic environmental factors would differ among colonies, resulting in differences in food provisioning and chick growth rates among the study regions. Thus, the phenotypic plasticity driven by differences in prey availability and, consequently, in foraging behavior may affect the provisioning of food resources during chick development and could contribute to the variation in body size observed among colonies.

It has been suggested that populations of seabirds are mainly regulated by food availability (Ashmole 1963; Weimerskirch 2002). In this sense, areas with high productivity could support larger colony sizes. However, on the other hand, in large colonies, density-dependent processes are exacerbated, and breeding success and recruitment decrease (Lewis et al. 2001; Pozzi et al. 2015). This pattern is because greater competition is present in larger
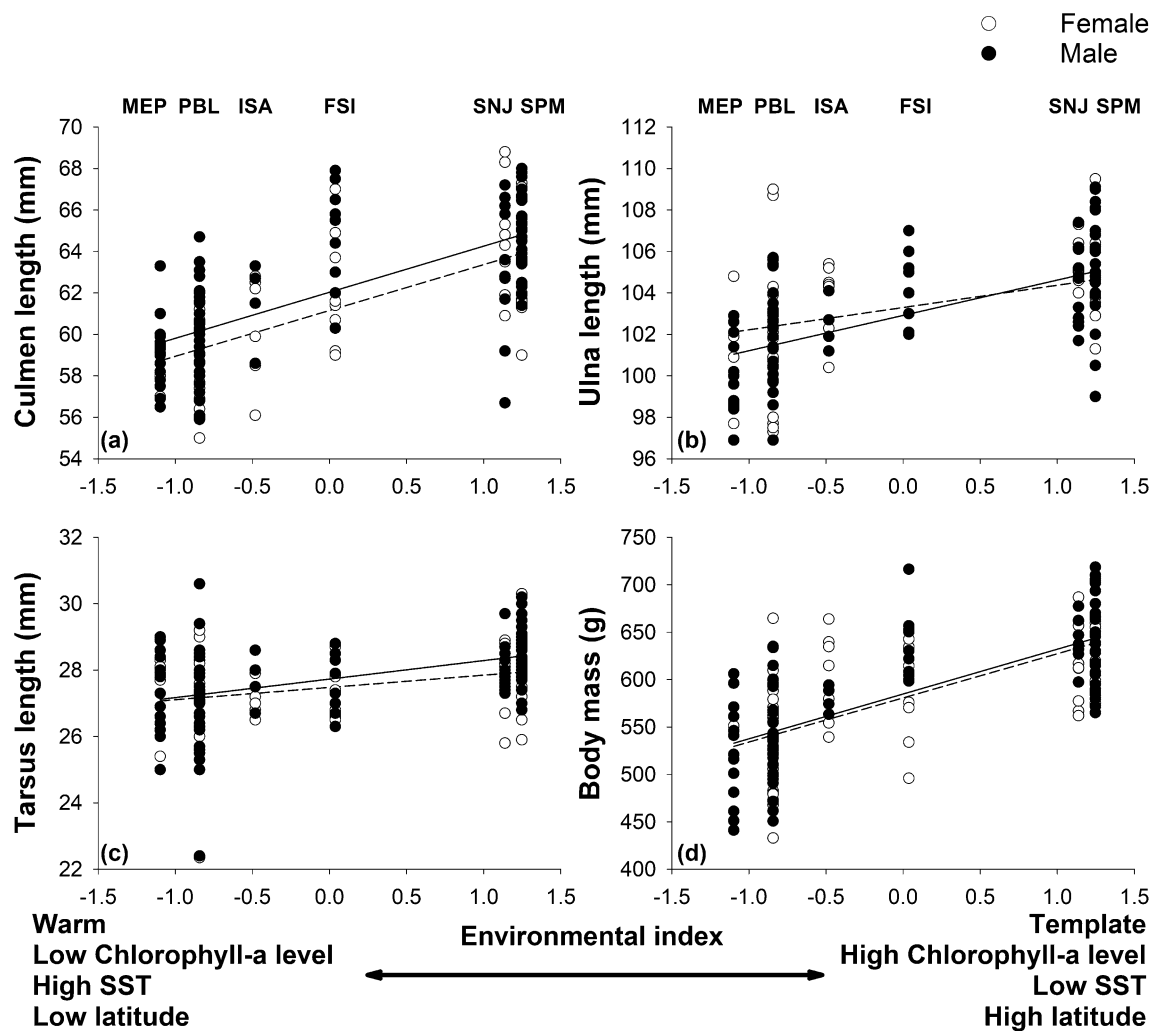
Fig. 3 Relationship between the environmental index and (**a**) culmen length (mm), (**b**) ulna length (mm), (**c**) tarsus length (mm), and (**d**) adjusted means of body mass (*g*) of females (*n* = 72; light dots) and males (*n* = 98; dark dots) of the red-billed tropicbirds in the study colonies. Regression lines estimated by the models used for female and male data sets are shown using dashed and solid lines, respectively. Study locations in the order shown in the figure: *MEP* = Morros El Potosí; *PBL* = Peña Blanca; *ISA* = Isabel; *FSI* = Farallón de San Ignacio; *SNJ* = San Jorge; *SPM* = San Pedro Mártir

colonies, and generally, less food or lower quality is given to the chicks compared to what is observed in smaller colonies. Thus, there could be a relationship between colony size and body size, although this pattern was not evident in preliminary analyses (see results in Table S2). The absence of a pattern may be due to multiple interacting factors that operate at different scales to regulate colony size, including biotic (e.g., predation, competition, and prey availability) and abiotic factors (e.g., availability of nesting sites, availability and extension of foraging grounds, wind speed, sea surface temperature, local climate conditions, and seasonality; e.g., Crespin et al. 2006; Amorim et al. 2009; Keslinka et al. 2019; Pagenaud et al. 2022).

Sexual size dimorphism (SSD)

Overall, the body trait data of red-billed tropicbirds did not support our prediction or the previously reported SSD pattern for the species. Instead, our results showed that individuals belonging to the SPM and FSI colonies were the only ones with significant SSD values (males > females; SSD index of 1.01–1.05 for significant body traits). This result partially agrees with those of Nunes et al. (2013), who determined that breeding males from the Abrolhos Archipelago were larger than females, specifically with regard to the wing chord (SSD index = 1.01) and bill measurements (bill length, nostril-to-bill-tip, and head-plus-bill; SSD index of 1.03, 1.01, and 1.01, respectively).

Many animal taxa exhibit SSD, including seabirds (Fairbairn and Shine 1993; Croxall 1995; Serrano-Meneses and Székely 2006). Latitudinal variations in SSD among populations within a given species have been found in vertebrate and invertebrate groups (Blanckenhorn et al. 2006; Roitberg 2007). Sex-specific selection for body size based on environmental factors (e.g., season length, food availability, or temperature) has been suggested to mediate the relationship between SSD divergence and latitude (Blanckenhorn et al. 2006; Roitberg 2007). However, the underlying mechanisms are often unclear, such that any latitudinal change in an environmental factor that affects one sex more than the other may generate sex-specific variations in body size and consequently affect SSD (Dobson and Wigginton 1996; Blanckenhorn et al. 2006; Tamate and Maekawa 2006; Roitberg 2007). Red-billed tropicbirds appear to partially conform to this pattern, as our study found male-biased SSD in northern colonies with enhanced levels of primary productivity.

The causes behind SSD have long been discussed, yet no definitive consensus has been reached. Currently, three principal hypotheses have been proposed to produce and maintain SSD: (1) sexual selection, (2) fecundity selection, and (3) differential niche-utilization, with the former being the most strongly supported mechanism to explain sexual dimorphism (Andersson 1994; Fairbairn 1997; Figuerola 1999; Serrano-Meneses and Székely 2006). It has been proposed that sexual selection favors smaller male body sizes in species with aerial displays, while larger body sizes are advantageous in species whose males either display or fight on the ground (Figuerola 1999; Székely et al. 2000; Serrano-Meneses and Székely 2006). In this context, sexual selection might be expected to favor larger males in red-billed tropicbirds because aerial displays are conducted in groups that likely involve both sexes (Nelson 2006), although individuals on the ground engage in intense fights and threats when competing for nest hole sites (e.g., Ascension Island; Stonehouse 1962).

In our study, it was expected that not only the SPM and FSI colonies would exhibit SSD but that other colonies with similar or larger population sizes would also exhibit SSD (e.g., PBL is a fivefold larger colony with an island surface area that is smaller than those of the others; Table 1). When competition for nesting crevices is frequent, sexual selection should favor larger males. Hence, sexual selection is not likely the primary mechanism driving the observed SSD in this study. On the other hand, the fecundity selection hypothesis may be ruled out for this species because our results show male-biased SSD, which is the opposite of what is expected with this hypothesis proposed to explain female-biased SSD.

It is essential to mention that the pattern of SSD found in red-billed tropicbirds seems to follow the same pattern as those observed in other seabirds distributed in the Southern Hemisphere (both at intra-specific and family levels; Fairbairn and Shine 1993). For example, Fairbairn and Shine (1993) found that males tended to be larger than females in populations with large average body mass values whose individuals fed in highly productive oceanic areas, especially at high latitudes. However, further studies have shown that body size, SSD, and primary productivity are highly correlated, and applying multivariate analysis to such variables is not appropriate due to co-linearity (Croxall 1995; Serrano-Meneses and Székely 2006). From the results obtained in this study, SSD may be affected by a body size cline because SSD has also been shown to vary geographically in many species (Blanckenhorn et al. 2006; Bidau et al. 2016). Under this scenario, it may be established that environmental variability influences body size and SSD. However, identifying the underlying mechanisms will require further studies that evaluate latitudinal variation due to sex-specific, natural, and sexual selection on body size.

Overall, our results indicate that the body size of red-billed tropicbirds breeding in the Mexican Pacific shows a latitudinal cline, which could be influenced by a set of both abiotic (i.e., air temperature, SST and chlorophyll-a) and biotic (i.e., food availability and foraging behavior) factors that are not mutually exclusive. Furthermore, the SSD detected in two colonies with relatively large mean body sizes, high chlorophyll-a values, and low SST values suggest that variation in productivity among populations could be an essential correlate or mediator of SSD, and future studies should assess whether or how latitudinal variation in body size is related to sex-based size differences and their putative selective causes. In other species, it has been established that there is a relationship between body size, foraging behavior, and fitness (Barbraud et al. 1999). Then, to understand the ecological and evolutionary significance of the body size variation in red-billed tropicbirds is necessary to know the foraging behavior and breeding success under different environmental regimes at different colonies.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The fieldwork, including wildlife management and sampling collection, was conducted with permission from the Dirección General de Vida Silvestre (DGVS, Mexico) under the permits SGPA/DGVS/62712/12, SGPA/DGVS/02923/13, SGPA/DGVS/00404/15, and SGPA/DGVS/02779/21. We complied with all applicable institutional and/or national guidelines for the welfare and conservation of wildlife. All individuals included in this study were not handled for more than 10 min, and the smallest amount of blood was drawn from each individual. While the adults were sampled, we cared for their eggs and/or chicks until their parents returned to the nest. No individuals abandoned their nests after capture.

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