



Parental duties and foraging strategies of a tropical pelagic seabird (*Phaethon aethereus*, Aves: Phaethontidae) during the breeding season

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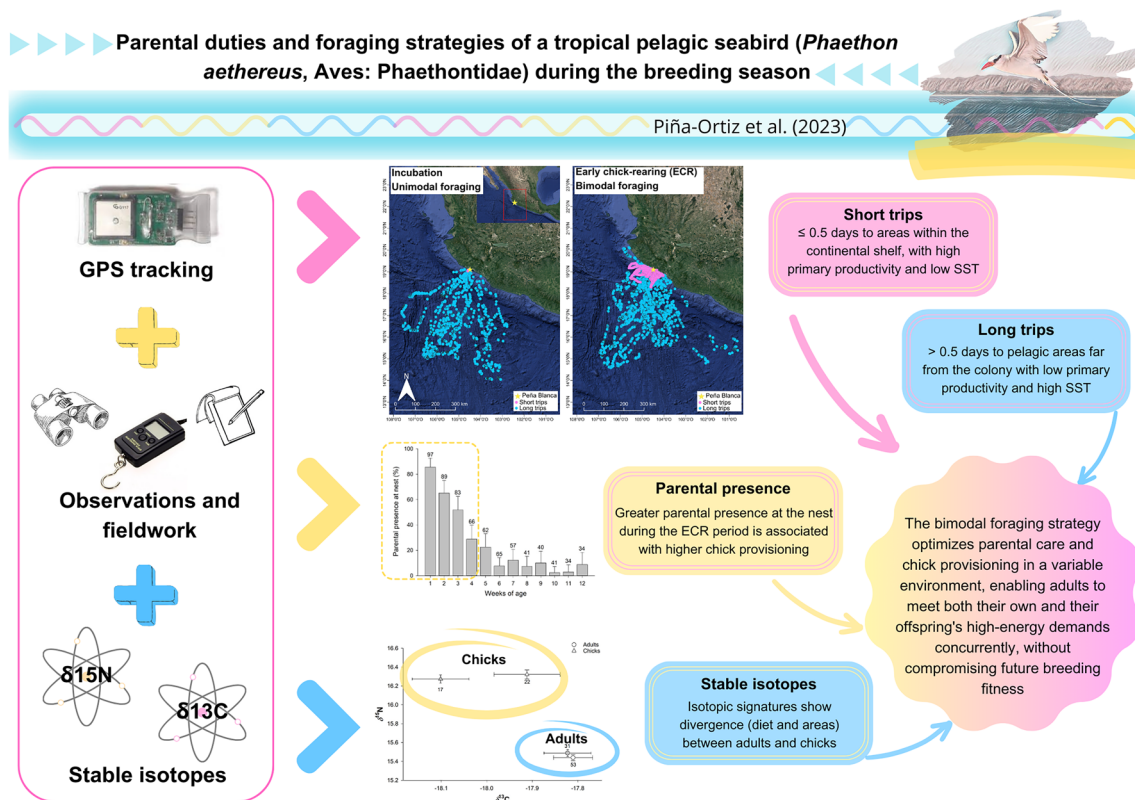
Abstract

Breeding seabirds must balance the energetic demands of feeding themselves and their offspring while coping with the constraints imposed by central-place foraging. As such, foraging strategies and parental care patterns are usually linked. Here, the foraging behavior of the Red-billed Tropicbird (*Phaethon aethereus*; n = 161) of Peña Blanca Islet, Mexico (19° 06' 11" N, 104° 29' 12" W) during the incubation and chick-rearing (≤ 4 weeks of age) stages was characterized with the aid of GPS loggers. Blood samples from adults and chicks were collected to determine $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, and parental presence at the nest, meal size, and parent-chick feeding events were recorded. During incubation, parents made long trips offshore to areas far from the colony; however, immediately after their chicks hatched, the parents switched to a bimodal foraging strategy by undertaking both short and long foraging trips. The $\delta^{15}\text{N}$ values indicated that trophic differences were present between parents and their offspring, with chicks being fed prey enriched in ^{15}N . Parental presence at the nest was greater during early chick-rearing, which was associated with a higher provisioning rate. Parents adopted a strategy in which the parent on nest duty only made short foraging trips to provide for its offspring without leaving it unattended for long periods, while its mate undertook long trips to feed itself. After the early chick-rearing period, the parents gradually reduced the time spent at the nest and increased the time spent foraging, compensating with larger meal sizes for their offspring.

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Extended author information available on the last page of the article

Graphical abstract



Keywords Bimodal foraging · Foraging behavior · GPS-tracking · Parental duties · Red-billed Tropicbird · Stable isotopes

Introduction

The breeding season is an essential and energetically demanding period in the annual cycles of seabirds. During this period, seabird parents must strike a balance between feeding themselves and their offspring given the constraints of central-place foraging (Orians and Pearson 1979; Harding et al. 2013; Cleeland et al. 2014). In the marine environment, resources are generally sparse and patchy, making it difficult for pelagic seabirds to gather enough food for themselves and their chicks (Weimerskirch 2007; Shoji et al. 2015). If food resources in the vicinity of a seabird breeding site are limited, parents may be unable to simultaneously meet the needs of their offspring while maintaining their body condition (Welcker et al. 2009). In response to this limitation, seabird species can employ a bimodal foraging strategy, which has been reported in the families Laridae, Sulidae, Spheniscidae, Diomedidae, Procellariidae, Alcidae, Fregatidae, and Phaethontidae (Baduini and Hyrenbach 2003; Steen et al. 2007; Welcker et al. 2009; Sommerfeld and Hennicke 2010; Campos et al. 2018; Austin et al. 2019; Phillips et al. 2023).

The bimodal foraging strategy is characterized by either alternating short and long trips or long trips interspersed with multiple short trips (Weimerskirch 1998; Congdon et al. 2005). Short trips enable parents to feed their chicks frequently, albeit at the expense of adult body condition, while long trips allow the adults to restore their reserves (Weimerskirch 1998; Weimerskirch et al. 2003). However, this bimodal foraging strategy may be influenced by the distance of profitable prey patches from the colony (Suryan et al. 2000). The bimodal foraging strategy has also been interpreted as a means of regulating parental investment in offspring (Granadeiro et al. 1998). Originally, the decision to undertake a short or long trip was thought to be under the exclusive control of parental body condition (Weimerskirch 1998). However, chick begging was found to strongly influence seabird parents in later studies (e.g., Quillfeldt 2002; Hamer et al. 2006), although its influence on bimodal foraging has not been investigated. The bimodal foraging strategy is relatively common among seabirds distributed in temperate and tropical-subtropical areas, and the factors affecting

the decisions of the parents to undertake either long or short foraging trips may be species-specific (Baduini and Hyrenbach 2003).

The Red-billed Tropicbird (*Phaethon aethereus*) is a pelagic seabird distributed in the tropical areas of the Atlantic, Indian, and Pacific Oceans (Nelson 2006). This species exhibits foraging plasticity in response to the varying oceanographic conditions in its breeding sites (Castillo-Guerrero et al. 2011; Diop et al. 2018). In the eastern Pacific, red-billed tropicbirds live in the open ocean most of the year, where they forage in patchy oligotrophic waters characterized by shallow thermoclines and low salinity (Spear and Ainley 2005). During the breeding period, which lasts approximately six months, they become central-place foragers, alternating between tending to their chicks in nesting colonies and undertaking foraging trips that take them up to 600 km from their breeding sites (Nelson 2006; Diop et al. 2018).

During the rearing period, parents must feed their chicks frequently. In turn, parents exploit the trophic resources surrounding the colony by undertaking short foraging trips lasting 3–4 h (Sommerfeld and Hennicke 2010; Campos et al. 2018). Nevertheless, the amount of available food near these colonies may be insufficient to maintain parental body condition and meet the needs of growing chicks. In response, red-billed tropicbirds appear to switch from a unimodal to bimodal foraging strategy (see Sommerfeld and Hennicke 2010). Nevertheless, it is unknown whether the use of a bimodal foraging strategy is widespread among tropicbirds or if it is employed only by individuals in breeding colonies located in highly oligotrophic environments or during years of low prey availability (Campos et al. 2018). Furthermore, little information is available regarding the habitat use, behavior, or foraging ecology of the Red-billed Tropicbird (e.g., Diop et al. 2018; Madden et al. 2022, 2023). Indeed, no study has linked foraging variables to Red-billed Tropicbird breeding parental presence at the nest, meal mass, chick-feeding rates, or foraging behavior at sea.

In this study, we assessed the foraging ecology and parental care patterns of breeding red-billed tropicbirds on Peña Blanca Islet, Mexico. We characterized the foraging areas surrounding the islet and their oceanographic characteristics, including sea surface temperature (SST), chlorophyll-a (Chl-a), and bathymetry, and monitored the at-sea behavior of red-billed tropicbirds during the egg incubation and chick-rearing stages with the aid of GPS data loggers over six breeding seasons (2017–2022). In addition, we measured the isotopic values of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in whole blood samples from adults and chicks to evaluate if differences were present in the assimilated foods. The presence of parents at nests, feeding frequency, and amount of food given to chicks were also evaluated, considering the age of the chicks. We hypothesized that (1) breeding adults

would switch from a unimodal to bimodal foraging strategy between the incubation and chick-rearing stages, undertaking more short than long trips during the latter stage; (2) the bimodal strategy would allow for a high parental presence at the nest and frequent chick feeding during the first weeks after hatching, which would be reflected in the presence of at least one parent at the nest, who would be in charge of undertaking short trips to provide food for the chick, while its mate would undertake long trips for self-provisioning; (3) variations in isotopic composition would be present between the blood of parents and their offspring, with chicks showing enriched $\delta^{15}\text{N}$ values and impoverished $\delta^{13}\text{C}$ values compared to those of their parents because chicks would be fed prey from high trophic levels found in areas near the colony; (4) a gradual decrease in adult presence at the nest would be apparent along with an increase in foraging activity, which would be reflected in an increase in chick meal size as the chicks grew.

Materials and methods

Study area

The study was carried out on Peña Blanca (19° 06' 11" N, 104° 29' 12" W), an islet located 1.9 km from the coast of Colima, Mexico (Supplementary Information, Fig. S1). Peña Blanca supports a colony of 1200–1600 pairs of red-billed tropicbirds (Hernández-Vázquez et al. 2018). According to the climatic conditions and primary productivity of the sea in the region, there are two marked climatic periods during the year: winter-spring (Dec–May) and summer-autumn (Jun–Nov). During winter-spring, SST values range between 23.5 and 30 °C, while salinity (34.3) and Chl-a (up to 10 mg m⁻³) are both high at the beginning of the period, with Chl-a later decreasing (1 mg m⁻³). Summer-autumn is characterized by high SST values that increase to 31 °C, while salinity and Chl-a values decrease to 33.5 and ~0.1 mg m⁻³, respectively (Kono-Martínez et al. 2017). The topographic and physiographic features of the coast promote the formation of dynamic mesoscale structures (i.e., marine current systems spanning 1–100 km), such as anticyclonic and cyclonic eddies, over the continental shelf (Salas et al. 2006).

GPS deployment and sampling

Fieldwork was conducted from January to May during six consecutive breeding seasons (2017–2022; Table S1), covering the egg-laying peak (Jan–Feb) and hatching and fledging periods (Mar–Apr) of this colony (Hernández-Vázquez et al. 2018). GPS data loggers (i-gotU GT-120, Mobile Action, Taiwan; CatLog-S, Catnip Technologies, Hong

Kong, China; and CatLog-S2, Perthold Engineering LLC, Dallas, USA) were attached to 161 breeding adults, which were captured by hand directly from nest burrows during incubation and the first 4 weeks of the chick-rearing period (early chick-rearing; ECR). Each nest was located within a pre-established study plot used for long-term monitoring. The loggers were programmed to record time, latitude, and longitude every 5 min and water-proofed with heat-shrink casing.

Data loggers were attached with TESA® tape (Norderstedt, Germany) to the tops of four to five central rectrices directly below the uropygial gland. The loggers and tape weighed between 8–16 g, which was ~2.4% (1.5–2.9%) of adult body mass (536.85 ± 50.56 g; range: 432.9–664.6 g, $n=54$; Piña-Ortiz et al. 2023) and below the recommended 3% weight threshold for devices attached to birds (Wilson and McMahon 2006; Vandenabeele et al. 2012). Adults from targeted nests were captured during the first hours of daylight (0600–0900 h) and the last hours before dusk (1800–2000 h) to protect the birds from sunstroke. The handling time never exceeded 10 min. Data loggers were recovered 1–15 days after being attached by carefully removing the tape from the tail feathers. In addition, blood samples (~0.5 mL per bird) were obtained by brachial vein puncture with a syringe (3 mL, 23G, 0.5 mm × 16 mm) from adults ($n=84$) and chicks ($n=39$), including those tagged with GPS devices during the 2020–2022 breeding seasons. The blood samples were transferred to 1.5-mL plastic tubes and kept on ice in the field. Once in the laboratory, they were frozen at -20 °C for stable isotope analysis. While the adults were handled, assistants cared for the eggs or chicks until the adults were returned to the nests. Continual monitoring of the nests and parental breeding success confirmed that no adults abandoned the nests after being handled.

Analyses of foraging trajectories

We visually reviewed every GPS trajectory obtained from all individuals in Google Earth or CatLog_Data-viewer and removed all anomalous trajectories and those over land. Next, following the approach applied by Diop et al. (2018), we eliminated those fixes that would have resulted in an average velocity of > 80 km h⁻¹ (i.e., the species flight speed threshold). Then, foraging parameters from the tracking data were determined in R v. 4.3.1 (R Core Team 2023) with RStudio v. 2023.06.1 + 524 “Mountain Hydrangea” (RStudio Team 2023) using the function ‘tripSplit’ provided in the ‘track2KBA’ package (Beal et al. 2021). This function allowed us to split individual GPS trajectories from multiple foraging trips from individual birds, which were separated by the return of the individual to the colony. For each foraging trip, we calculated the maximum linear distance from the colony, the total duration of the trip, and the total distance

traveled. Incomplete foraging trips (i.e., foraging trips that could not be fully tracked prior to the return of an individual to the colony) were removed from all subsequent analyses. To guarantee the accurate splitting of individual foraging trips, given that subsequent trips with burrow-nesting species may be lumped into a single trip, a 1.5-km radius filter was applied to the colony to discard these locations (Beal et al. 2021).

A total of 178 complete foraging trips were recorded from 140 Red-billed Tropicbirds during the incubation and ECR stages from 2017 to 2022 (Table S1). Individual foraging trips were classified as either short (≤ 0.5 days) or long (> 0.5 days) using the method proposed by Welcker et al. (2009), who used two log-normal distributions to determine the best fit and set the cut-off value as that which minimized the sum of the variances of both trip types given their log-normal distribution. For subsequent analyses, data from all years were pooled according to the lowest number of complete foraging trips for 2017, 2018, and 2019 (3, 3, and 12 trips, respectively; Table S1, Fig. S1).

Once all individual foraging trips were classified, they were grouped based on behavior with Hidden Markov Models (HMM) with the ‘moveHMM’ package (Michelot et al. 2016). Four behavioral states were defined based on the speeds and turning angles of the trajectories: resting (low speed and low turning angles), intensive search (low speed and high turning angles), extensive search (high speed and high turning angles), and relocation (high speed and low turning angles). Similar to what has been obtained in other studies that have classified the foraging behavior of tropicbirds (see Diop et al. 2018), the HMM algorithm does not effectively categorize intensive search and resting behaviors (Fig. S2–S5). Therefore, fixes classified as intensive search and resting behaviors were grouped into the single category of “resting-intensive search”. Foraging behavior was then inferred from locations classified as “extensive search” and “resting-intensive search”. Extensive searches involved individuals foraging over large areas to locate prey patches, whereas intensive searches occurred when individuals conducted area-restricted searches after locating prey (Weimerskirch 2007; Bennison et al. 2017; Clay et al. 2019; dos Santos et al. 2022). Subsequently, “extensive search” and “resting-intensive search” locations were selected to classify the habitat use of red-billed tropicbirds using kernel density estimations (KDEs) through the transformation of all positions into utilization distributions (Wood et al. 2000).

To estimate the kernel utilization distributions (KUD), we made use of the functions ‘hr_kde_ref’ and ‘hr_kde_pi’ in the ‘amt’ package (Signer et al. 2019) to calculate the reference bandwidth and the bandwidth with the plug-in equation method in two dimensions, respectively (Wand and Jones 1994; Gitzen et al. 2006). Due to its simplicity and wide use in other studies, we selected the reference bandwidth as

the ideal smoothing parameter for estimating KUDs (Beal et al. 2021). A smoothing parameter of 6.75 km was used for short trips, and a smoothing parameter of 27.89 km was used for long trips. We calculated the 50% and 95% KUDs using the function 'hr_kde' in the package 'amt' to represent the core and general foraging areas used by adults, respectively (Fig. S6). The representativeness (the degree to which the space use of a tracked sample of animals represents that of the larger population) of short and long foraging trips was tested separately for the incubation and ECR stages, resulting in a low representativeness for the population (Fig. S7–S8). However, the representativeness for short and long foraging trips pooling both breeding stages was suitable (Fig. S9–S10; Beal et al. 2021). The overlap of the KUD contours for core areas between short and long trips was calculated with the function 'hr_overlap' using the utilization distribution overlap index (UDOI). The UDOI ranges from 0 (when two home ranges do not overlap) to 1 (when two utilization distributions are uniformly distributed and show 100% overlap). However, the UDOI can be > 1 if the utilization distributions are non-uniformly distributed and exhibit a high degree of overlap (Fieberg and Kochanny 2005).

Oceanographic variables

The oceanographic characteristics of the core areas (KUD 50%) of short and long foraging trips were assessed. Raster data for SST ($^{\circ}\text{C}$), Chl-a (mg m^{-3}), and bathymetry (m) were downloaded from the ERDDAP database (<http://coastwatch.pfeg.noaa.gov/erddap>). The SST and Chl-a values were collected from the Aqua MODIS satellite model "Net Primary Production (NPP), 0.025 degrees, Pacific Ocean, Daytime, 2006–present (8 Day Composite), Lon \pm 180." Bathymetry values corresponded to the model "Topography, ETOPO1, 0.0166667 degrees, Global (longitude -180 to 180), (Ice Sheet Surface)." The raster images used for SST and Chl-a had a monthly period from December to May between 2017 and 2022, which were the months during which the foraging tracks were recorded (Hernández-Vázquez et al. 2018). Finally, the values of the oceanographic variables within each core area (i.e., short and long trips) were obtained.

A Chi-square homogeneity test was used to compare the proportion of short and long foraging trips between the incubation and ECR stages. Two-way analyses of variance (ANOVA) were used to compare SST values and Chl-a concentrations between the core areas, including the type of foraging trip (i.e., long or short) and month as categorical factors. Bathymetry differences between the core areas were tested with a one-way ANOVA with the type of foraging trip as a factor.

Parental presence

The presence of parents caring for chicks at the nests was based on the results of monitoring 68, 108, and 100 nests during December–April of the 2020, 2021, and 2022 breeding seasons, respectively. The number of active nests, chick age, and the presence or absence of the parents were recorded within pre-established study plots by punctual observations of all nests in these plots. The time required to survey all pre-established plots was approximately 4 h (0800–1100 h), and the plots were surveyed in the same order each time. We knew the hatching dates for most chicks; however, when hatching occurred between visits, chick age was estimated based on plumage and body measurements. In the 2020 season, we conducted 5 surveys (3 December, 28 January, 10 February, 9 and 21 March). In the 2021 and 2022 seasons, we conducted 9 and 8 surveys during each season (2021: 18 December; 15, 22 and 31 January; 9 and 16 February; 19 and 27 March; and 4 April; 2022: 12 and 14 December; 18 and 24 January; 1 February; and 11, 22, and 31 March), respectively. On Peña Blanca, red-billed tropicbirds are not sexually dimorphic; thus, it was not possible to sex the adult individuals. However, to identify each member of a breeding pair, individuals were tagged with alphanumeric bands affixed to the tarsus.

Stable isotope analyses

To assess differences in the assimilated foods between parents and offspring, carbon and nitrogen isotope analyses were conducted on whole blood samples that reflected the dietary integration period of 2–4 weeks prior to sampling (Bearhop et al. 2002). Therefore, the blood samples taken from the individuals in this study during the ECR (adults = 53 [2020 = 15, 2021 = 16, and 2022 = 22], chicks = 17 [2020 = 5, 2021 = 1, and 2022 = 11]) and late chick-rearing (LCR; adults = 31 [2020 = 8, 2021 = 11, and 2022 = 12], chicks = 22 [2020 = 9, 2021 = 3, and 2022 = 10]) periods should reflect the dietary items consumed during those stages. Blood samples were oven-dried at 50°C for 24–48 h and then finely ground and homogenized. Subsamples (0.3–0.5 mg) were packed in tin capsules and analyzed for %N, %C, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ using a Flash 2000 elemental analyzer (Thermo Scientific, Milan, Italy) coupled with a Delta V Plus isotope ratio mass spectrometer with a ConFlo IV interface (Thermo Scientific, Bremen, Germany). Analyses were conducted at the Littoral, Environnement et Sociétés (LIENSs) Joint Research Unit stable isotope facility (CNRS – La Rochelle Université, France). Results are expressed as δ (‰) for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and were calibrated against the international isotopic references of atmospheric nitrogen for $\delta^{15}\text{N}$ and Vienna-Pee Dee Belemnite for $\delta^{13}\text{C}$. The analytical precision was ± 0.15 ‰ $\delta^{15}\text{N}$ and ± 0.10

‰ for $\delta^{13}\text{C}$ based on the internal standards USGS-61 and USGS-62, which were inserted every ten measurements. All samples had low C:N mass ratios (<4.0), indicating low lipid content, and no lipid extraction was required (Cherel et al. 2005).

Physiological and metabolic differences between seabird adults and chicks may influence their isotopic ratios (Harding et al. 2008; Sears et al. 2009; Micklem et al. 2021). Therefore, the isotopic composition between parents and offspring may reflect some differences not linked to dietary intake. As chicks grow, their $\delta^{15}\text{N}$ values gradually change due to ontogenetic changes in tissue turnover rates (Harding et al. 2008; Sears et al. 2009; Micklem et al. 2021). Blood analyses of captive African penguins (*Spheniscus demersus*) showed that chick growth resulted in a depletion of ^{15}N in whole blood of 0.30 ‰ with respect to that of the adults (neither breeding, fasting, nor molting) under the dietary regime established by the researchers (see Micklem et al. 2021 for details). To compare adult and chick $\delta^{15}\text{N}$ values, we adjusted our $\delta^{15}\text{N}$ data by subtracting 0.30 ‰ from the adult values.

General linear models (GLM) were used to assess the differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope ratios between chicks and adults (i.e., age class), including the effects of the breeding season (2020–2022) and breeding stage (ECR and LCR) as factors and sample collection date (days since 1 January) as a continuous predictor. All GLMs were applied based on complete initial models that considered all variables and interactions. Subsequently, all non-significant interactions and variables ($P < 0.05$) were eliminated to simplify the models. The initial models, which included all variables and interactions, are presented in Table 3. However, the accompanying statistics correspond to the level at which non-significant interactions and variables were removed from the model.

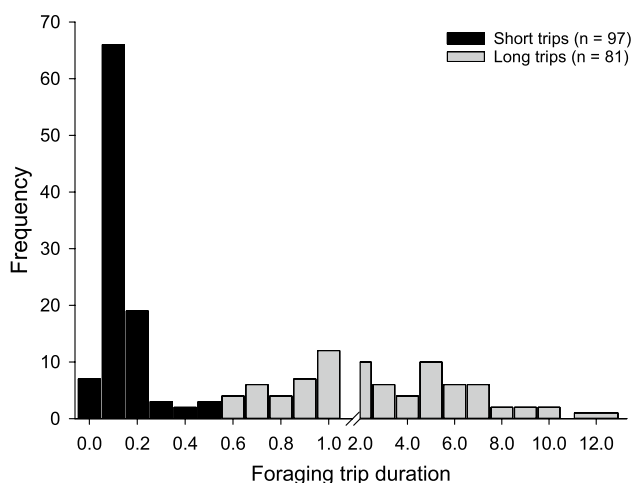


Fig. 1 Frequency distribution of foraging trip duration (days) of the Red-billed Tropicbird of Peña Blanca Islet, Mexico. Short trips are indicated by dark bars, and long trips are indicated by gray bars

Table 1 Number and proportion of long and short foraging trips in red-billed tropicbirds in the incubation and early chick-rearing (ECR) stages from 2017 to 2022 at Peña Blanca Islet, Mexico

Foraging trip length	Incubation <i>n</i> = 11		Early chick-rearing <i>n</i> = 167	
	Number of trips	Proportion (%)	Number of trips	Proportion (%)
Long	10	90.9	71	42.5
Short	1	9.1	96	57.5

A Chi-square test revealed significant differences in the distribution of the number of long and short foraging trips between the incubation and ECR stages (Chi-square test, $X^2 = 7.90$, $df = 1$, $P = 0.005$)

Furthermore, t-tests that included a Bonferroni correction ($\alpha = 0.025$, 2 comparisons) were used to compare differences in isotopic signatures between adults and chicks during the ECR and LCR stages.

Chick feeding events

Parental food supply and chick meal sizes were determined in the 2020, 2021, and 2022 breeding seasons by weighing 82 chicks (1–12 weeks old) three times (events) each day at dawn (0700 h), noon (1300 h), and dusk (1800 h). Chick body mass was measured with a portable electronic scale to the nearest 5 g. For each breeding season, chicks were selected from nests located in five different islet sections exhibiting different nest densities. Body mass was measured in 34, 20, and 28 chicks in either March or April of 2020 (13–20 March), 2021 (27 March–2 April), and 2022 (23–31 March), respectively. The maximum number of nests with chicks and the highest annual values of Chl-a surrounding the study area are present during these months (Hernández-Vázquez et al. 2018). For each time event, the weighing time was ~40 min, and each chick was always weighed in the same order. Increases in chick mass between weighing events were attributed to parental feeding and were used to estimate daily feeding events and meal sizes.

Due to the sensitivity of the scale and the unlikelihood of adults feeding chicks with only small amounts of food, all increases in weight < 10 g were omitted from the analyses. To obtain the number of feeding events per day, we divided the number of events in which a chick gained weight by the number of days it was weighed. Mass increments between weighing events can be considered a proxy of the meal sizes parents deliver. However, with this approach, the amount of food is inevitably underestimated because chicks also lose mass through excretion. Therefore, we evaluated mass loss after feeding events using linear mixed models (LMMs), to estimate the relationship between chick mass loss rates at

Table 2 Foraging and spatial ecology parameters (mean \pm SD) of red-billed tropicbirds on short and long trips during incubation and ECR stages at Peña Blanca Islet during six consecutive breeding seasons (2017–2022)

Foraging parameters	Short trips	Long trips
<i>n</i> =	41	49
Number of foraging trips	97	82
Trip duration (days)	0.1 \pm 0.1	3.7 \pm 2.9
Maximum distance to colony (km)	31.1 \pm 21.3	245.8 \pm 173.1
Total distance travelled (km)	75.3 \pm 52.7	771.8 \pm 554.6
Direction (°)	228.2 \pm 55.6	205.8 \pm 51.6
Spatial ecology parameters		
Number of foraging trips	39	35
Core areas (50% KUD; km ²)	545.2 \pm 635.4	10,761.9 \pm 8072.4
General areas (95% KUD; km ²)	2169.1 \pm 2745.6	46,701.8 \pm 35,222.5
Core areas overlap between foraging trip category	2.24 \times 10 ⁻² \pm 0.0	
General areas overlap between foraging trip category	0.10 \pm 0.00	

Breeding season and reproductive stage data are pooled. Direction (°) was measured from the origin (islet) to the furthest point of the foraging trip. The overlap of the core areas (50% KUD) was estimated between trip categories using the utilization distribution overlap index (UDOI). *n* = number of individuals from which the foraging and spatial ecology parameters were obtained. The UDOI ranges from 0 (when two home ranges do not overlap) to 1 (when two utilization distributions are uniformly distributed and exhibit 100% overlap; Fieberg and Kochanny 2005)

post-feeding intervals and initial mass, chick age, and meal size, with individuals considered a random factor.

The rate of mass loss following a feeding event was related to the initial mass of the chick and meal size but not to chick age [ANOVA Satterthwaite's method, Meal size: $F_{(1,273)} = 11.90$, $P < 0.001$; Initial mass: $F_{(1,273)} = 7.45$, $P = 0.006$; Age: $F_{(1,273)} = 1.96$, $P = 0.16$]. The equation obtained, $Masslossrate(gh^{-1}) = -0.235 - 0.030(meal\ size) - 0.009(initial\ mass)$, was used to estimate mass loss between weighing events and correct the calculated meal size and the total amount of food provided to the chicks. Meal size corrections were made under the following extreme possibilities: (1) the maximum possible meal size, assuming that chicks were fed immediately before weighing, and (2) the minimum possible meal size (no adjustment required), assuming that the chicks were fed just after they were weighed. Considering

such possibilities, a consumption threshold (i.e., the range between these two possibilities) was obtained for each age group. In addition, we recorded culmen, ulna, and tarsus lengths for all chicks on both the first and last weighing days (Table S2). All statistical analyses were conducted in STATISTICA 7.1 (Hill and Lewicki 2007), except for the LMMs, which were implemented with the 'lme4' package in R (Bates et al. 2015). All values are expressed as mean \pm SD throughout the results section. The significance level was set to $P \leq 0.05$.

Results

Foraging strategy of breeding adults

Overall, the foraging trips exhibited a bimodal distribution, with more short trips (97 trips; up to 0.5 d) than long trips (81 trips; up to 12 d; Fig. 1). Short and long foraging trips were recorded for all breeding seasons (see Table S3). However, during the incubation period, tropicbirds conducted long trips > 90% of the time. After the eggs hatched, tropicbirds undertook long and short trips 42.5 and 57.5% of the time, respectively (Table 1). This pattern was consistent for both reproductive stages throughout the breeding season of the species (Fig. S1). Short trips took the tropicbirds 31 km from the islet, lasted 0.14 \pm 0.10 d (mean \sim 3 h, range 1.03–12.85 h, *n* = 97), and covered a mean total distance of \sim 75 km. Individuals on long trips traveled approximately 770 km (mean maximum distance from the colony of 245 \pm 173 km, *n* = 81), with these trips lasting from 0.60 to 12.3 d (Table 2). Most trips were conducted southwest of the islet (Table 2; Fig. S1). The core (50% KUD) and general (95% KUD) areas used by red-billed tropicbirds on long trips were an order of magnitude larger in size than those of the short trips (Table 2, Fig. 2 and S2).

The core area of the short trips was located over the continental shelf and exhibited mean SST values ranging from 25.5 to 28.5 °C and mean Chl-a concentrations as high as 14 mg m⁻³ (Fig. 3). In contrast, the long-trip core area was located in deeper waters with higher SST (27.5–29.0 °C) and lower Chl-a concentrations (< 1 mg m⁻³; Fig. 3) than those of the short-trip core area. The bathymetry and oceanographic variables were significantly different between the two core areas throughout the breeding seasons of the Red-billed Tropicbird in the study area (ANOVA, Depth: $F_{(1,5058)} = 534.13$, $P < 0.001$; SST: $F_{(5,181667)} = 238.46$, $P < 0.001$; Chl-a: $F_{(5,181775)} = 950.33$, $P < 0.001$; Fig. 3a–c). In addition, the overlap between the short- and long-trip core areas was minimal (2.24 \times 10⁻² \pm 0.00), underlining different spatial utilization related to trip type (Fig. 2, Table 2).

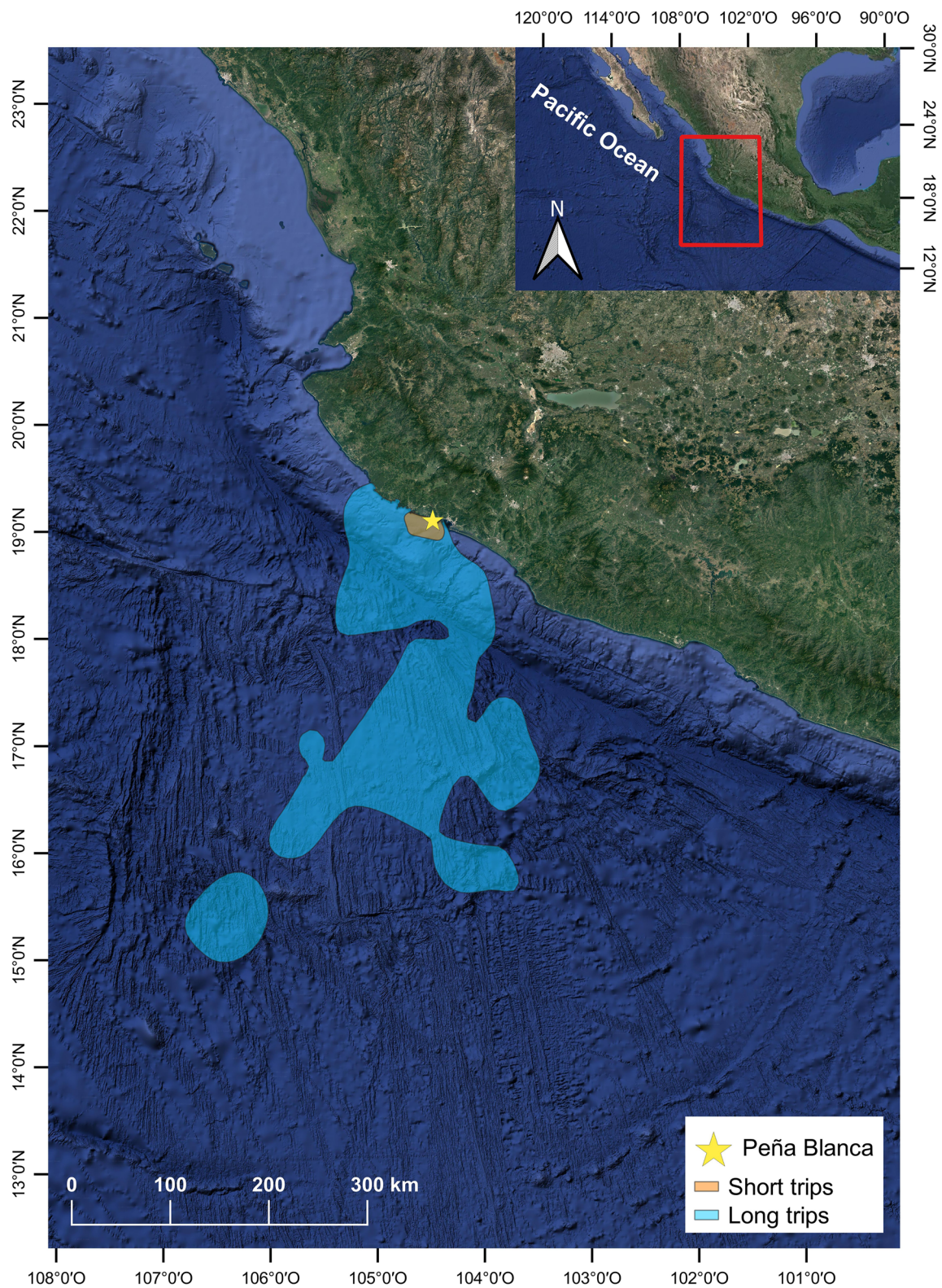


Fig. 2 Utilization distributions of core areas (50% KUD) used by red-billed tropicbirds on short and long foraging trips during the incubation and early chick-rearing (ECR) stages between 2017–2022 on Peña Blanca Islet, Mexico

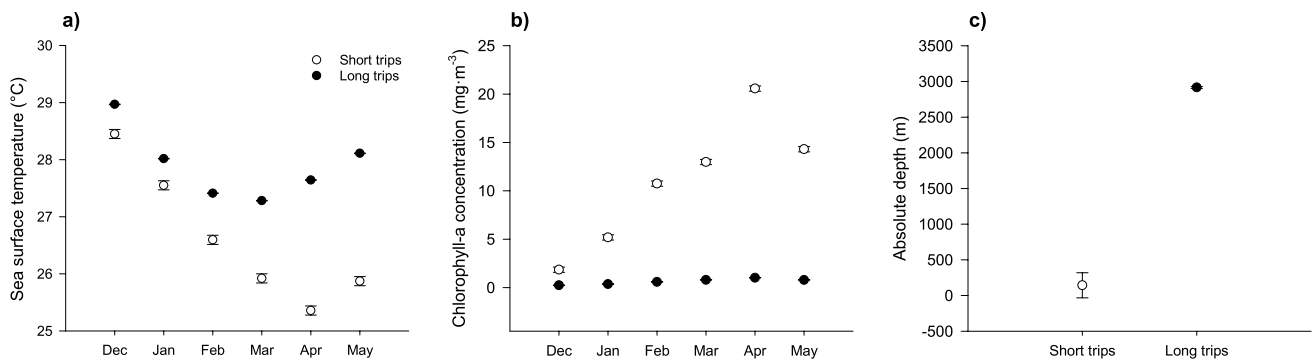


Fig. 3 Unweighted monthly mean \pm S.E. of **a** sea surface temperature, **b** chlorophyll-a concentrations, and **c** bathymetry (absolute value) in the core areas (50% KUD) of red-billed tropicbirds during short and

long foraging trips during incubation and early chick-rearing (ECR) stages over six breeding seasons (2017–2022) at Peña Blanca Islet, Mexico

Presence of adults at the nest

During nests checks, a total of 709 records (241 presence and 468 absence) allowed us to determine that parental presence gradually decreased during the first 4 weeks after chick hatching (86% during week 1, 29% during week 4). After the chicks reached 4 weeks of age, parental presence remained low until fledgling, fluctuating between 2–23% (Fig. 4a).

Variation in isotopic values between adults and chicks

The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values differed significantly between adults and chicks (GLM, $\delta^{15}\text{N}$: $F_{(1,116)} = 299.23$, $P < 0.001$; $\delta^{13}\text{C}$: $F_{(1,119)} = 16.10$, $P < 0.001$), with a significant year-stage interaction for $\delta^{15}\text{N}$ ($F_{(2,116)} = 5.10$, $P = 0.008$). The $\delta^{15}\text{N}$ values from ECR individuals in 2021 were higher than those from 2020 ($t = -0.35$, $P < 0.001$), and the values from LCR individuals during 2021 were higher than those from 2020 and 2022 (t-tests with Bonferroni correction, $t = -0.54$, $P < 0.001$ and $t = 0.50$, $P < 0.001$, respectively). Furthermore, the $\delta^{15}\text{N}$ values differed between these stages during 2021 ($t = -0.36$, $P < 0.001$). All other factors and interactions were not significant (Table 3). Chicks (in both the ECR and LCR stages) exhibited significantly higher $\delta^{15}\text{N}$ and lower $\delta^{13}\text{C}$ values than those of the adults (Fig. 5). The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of chicks were also consistent between years. Late-reared chicks had similar $\delta^{15}\text{N}$ values and slightly lower but not significantly different $\delta^{13}\text{C}$ values than those of early-reared chicks (Table 3; Fig. 5).

Meal sizes provided to the chicks

The chicks were fed more than once per day from 2–4 weeks of age, with the average amount of food they received not

exceeding 50 g per meal (Fig. 4b,c). From the fifth week of age onward, the chicks were fed approximately once per day, although the feeding frequency increased in weeks 7 and 9 and then continued to increase as the chicks approached fledgling age. The amount of food delivered to the chicks increased during the first 5 weeks and peaked in weeks 6–7, after which it gradually decreased (Fig. 4b,c). Chicks received between 8.5 to 127 g of food, with the greatest amount being given when the chicks were 5–7 weeks in age (Fig. 4c).

Discussion

Foraging strategy of breeding adults

This research demonstrates 1) Red-billed Tropicbird adults switch from unimodal to bimodal foraging strategies immediately after their chicks hatch, 2) the existence of different core utilization areas between adults on short and long foraging trips, 3) a pattern of parental presence in the nest during chick development, and 4) the presence of differences in the isotopic signatures of blood samples from adults and chicks during ECR and LCR. Adults appear to use short trips to feed chicks and long trips to feed themselves, indicating that bimodal foraging is bound to patterns of parental care. During the first few weeks of life, chicks require high parental presence at the nest and must be fed frequently, and consequently, parents take turns caring for their chicks. While one parent remains at the nest to care for its chick, making short trips to feed its offspring, its mate conducts long trips to feed itself. Adults gradually decrease the time they spend at the nest and increase the time they spend foraging. During this time, parents carry more food to their chicks as they grow, with the maximum chick meal sizes being delivered when the chicks are ~6 weeks old (Fig. 4c).

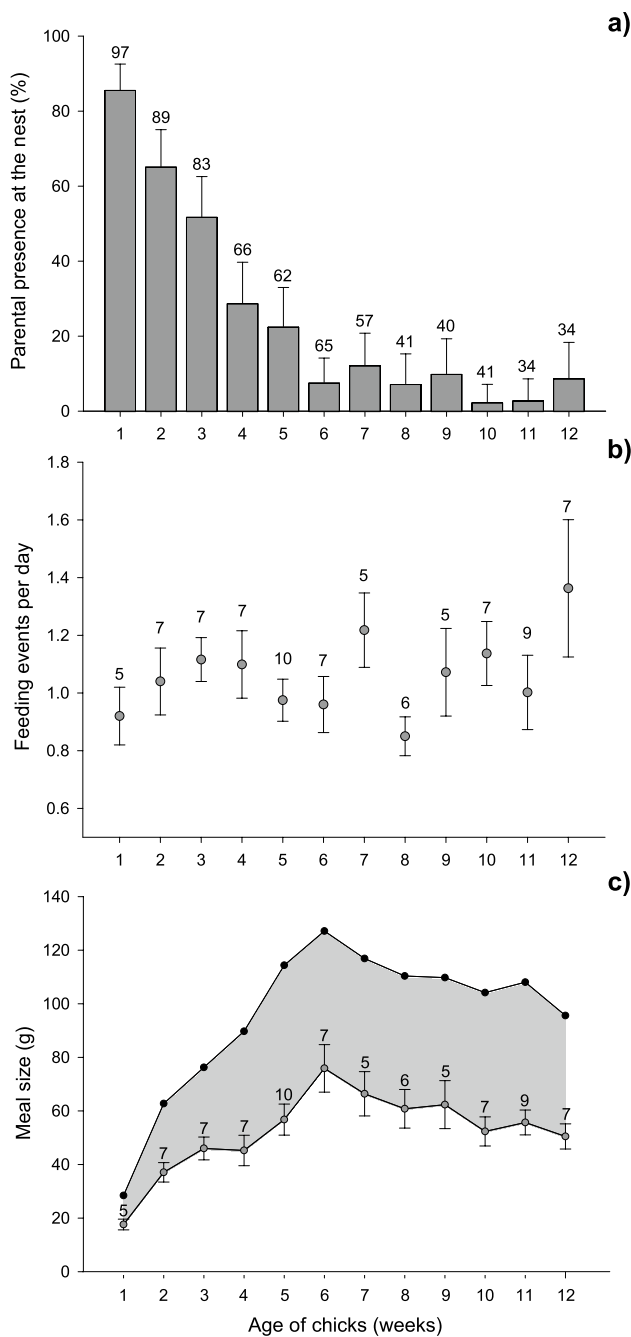


Fig. 4 Parental care and chick feeding of red-billed tropicbirds breeding on Peña Blanca Islet, Mexico. (a) Presence of the parents in active nests during the chick-rearing stage in the 2020–2022 breeding seasons; (b) mean \pm S.E. of chick-feeding rates per day; and (c) mean \pm S.E. of chick meal size, and fitted lines (black dots) of the total amount of food delivered to 1–12 week old Red-billed Tropicbird chicks (N=82) during the breeding seasons of 2020 to 2022. The gray shading represents the threshold between the minimum and maximum consumption estimates. The numbers above each error bar indicate the sample sizes from which the mean and S.E. were calculated [number of records for (a) and number of nests for (b) and (c)]

a) Bimodal foraging

Recent studies on the foraging ecology of red-billed tropicbirds have provided insights into their foraging grounds at-sea and colony-specific foraging movements (Diop et al. 2018; Madden et al. 2022, 2023). However, this study is the first to identify a bimodal foraging strategy during the chick-rearing period in this species (Fig. 1, Table S3). In other colonies, the frequency distribution of the duration of Red-billed Tropicbird foraging trips also shows a bimodal pattern during chick-rearing (see Fig. S12; data from Madden et al. 2022, 2023). Together these findings may indicate that bimodal foraging is an intrinsic mechanism of the species and perhaps even for Phaethontidae (Le Corre et al. 2003; Sommerfeld and Hennicke 2010; Campos et al. 2018; Phillips et al. 2023), instead of being adopted occasionally to cope with low resource availability or only by specific populations, as has been reported for other seabirds such as the Cory's Shearwater (*Calonectris borealis*; Granadeiro et al. 1998).

Bimodal foraging in which parents alternate or mix short and long trips is a behavioral strategy that is mainly implemented by pelagic seabirds (e.g., Procellariiformes, Alcids, Sphenisciformes, Suliformes, and Phaethontiformes) while caring for their chicks to meet the conflicting energy demands of self-maintenance and chick feeding (Weimerskirch et al. 1993, 1994; Weimerskirch 1998; Ropert-Coudert et al. 2004; Congdon et al. 2005; Steen et al. 2007; Welcker et al. 2009; Sommerfeld and Hennicke 2010; Saraux et al. 2011; Shoji et al. 2015; Campos et al. 2018, Austin et al. 2019; Phillips et al. 2023). Adult seabirds that engage in bimodal foraging are generally thought to make long trips to productive areas to feed themselves and avoid the high travel costs of commuting, whereas short trips to resource-poor areas near their nesting colonies are conducted to obtain resources for their offspring (Weimerskirch et al. 1994; Weimerskirch 1998; Jakubas et al. 2012; Welcker et al. 2012). Our findings indicate that red-billed tropicbirds follow this general pattern, making short trips (average of ~30 km) to areas around their colony and long trips (> 240 km) to pelagic areas far from the colony. However, during long trips, red-billed tropicbirds forage in areas with lower Chl-a concentrations and higher SST than those used during short trips (Fig. 3a,b).

Variation in isotopic values between adults and chicks

The different isotopic signatures in the blood samples from adults and chicks strongly suggest that parents and offspring consume different prey from different areas. In particular, parents fed their offspring with prey enriched in ^{15}N , which may be associated with elevated energetic content that could

Table 3 Summary statistics of the general linear models (GLMs) evaluating the effects of the breeding season, age class (adults and chicks), and reproductive stage (early chick-rearing, ECR; late chick-rearing, LCR) on the nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotope ratios measured in whole blood samples of red-billed tropicbirds from 2020 to 2022 at Peña Blanca Islet, Mexico

Comparison	$\delta^{15}\text{N}$			$\delta^{13}\text{C}$			
	Factors and interactions	F	df	p	F	df	p
Adults and chicks at ECR and LCR	Year-age class-stage	0.73	2, 110	0.49	0.66	2, 110	0.52
	Year-age class	0.16	2, 112	0.85	1.59	2, 114	0.21
	Year-stage	5.10	2, 116	0.008	1.34	2, 112	0.27
	Age class-stage	1.12	1, 115	0.29	2.34	1, 116	0.13
	Year	83.89	2, 116	<0.001	7.44	2, 119	<0.001
	Age class	299.23	1, 116	<0.001	16.10	1, 119	<0.001
	Stage	0.36	1, 114	0.55	1.83	1, 117	0.18
	Date	18.90	1, 116	<0.001	3.02	1, 118	0.09
		Date + age class + year + year-stage					
	Final selected model						

Sample sizes are as follows: Adults: ECR = 31; Chicks: ECR = 17, and LCR = 22. Initial models included all terms listed in the table. Significant terms were retained in the final models and are shown in bold

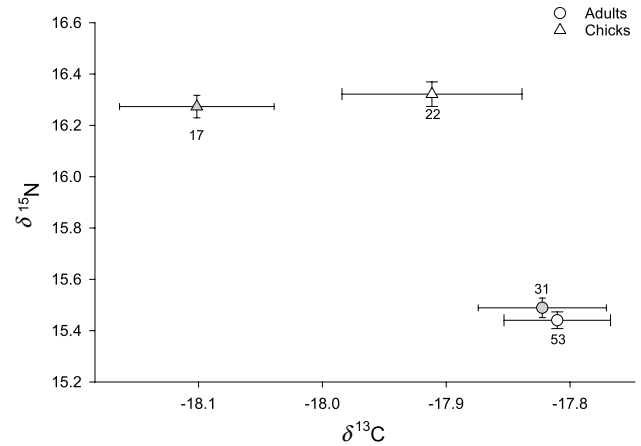


Fig. 5 Stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of whole blood in Red-billed Tropicbird adults and chicks during early chick-rearing (ECR; white symbols) and late chick-rearing (LCR; gray symbols) at Peña Blanca Islet, Mexico, during the breeding seasons of 2020 to 2022. Symbols differentiating adults (circles) and chicks (triangles) are shown. The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values represent means \pm SE. The number of samples analyzed is indicated next to each symbol. Adult $\delta^{15}\text{N}$ values were adjusted by subtracting 0.30 ‰ to account for metabolic differences between adult and chick seabirds

improve growth and body condition (Albano et al. 2011; González-Medina et al. 2017). The isotopic $\delta^{15}\text{N}$ composition differed by ~ 0.90 ‰ and 0.78 ‰ between adults and chicks during the ECR and LCR periods, respectively. Hence, the isotopic signatures are consistent with the change in feeding grounds exhibited by adult red-billed tropicbirds during the chick-rearing period being associated with the specific function of providing food and care to their offspring.

However, the question arises of why parents make long trips to less productive pelagic areas when short trips seem more profitable. Tropicbirds are distributed in tropical oceanic areas characterized by low resource productivity and predictability (Weimerskirch 2007). The use of both coastal and pelagic areas during the chick-rearing period could be linked to the energetic and nutritional demands of offspring, resource availability, and inter- and intraspecific competition for shared resources. According to the Chl-a values, a proxy of primary productivity, obtained during the study period and the relationship between areas with high primary productivity and fish and crustacean aggregation zones for spawning, rearing, and feeding (Franco-Gordo et al. 2008; Ambriz-Arreola et al. 2012; Capuzzo et al. 2017; Kozak et al. 2020), greater resource availability in foraging areas close to the colony was expected, as Chl-a values near the colony were higher than those offshore (Fig. 3b). Hence, utilizing areas near the colony requires less travel time, which would be reflected in more time spent caring for chicks and a regular food supply. However, this would involve a

trade-off because competition near the colony may also be high; therefore, the resource availability in these areas would likely be depleted at some point during the season (Birt et al. 1987; Weber et al. 2021). Thus, exclusively using nearby areas to obtain prey for chick provisioning would result in resources becoming scarce prior the chick is old enough for the parents to begin making longer trips.

On the other hand, foraging far from the colony may prove profitable for parents trying to maintain their own body condition, either because they are more successful in capturing prey far from the colony or because they encounter low competition, as has been observed in other tropical seabirds (Weimerskirch 1998; Austin et al. 2019). Peña Blanca supports approximately 2,500–3,300 breeding adults, without considering that several thousand other seabirds also breed on the islet and use nearby foraging areas (Hernández-Vázquez et al. 2017). These breeding adults exploit an area of ~550 km² surrounding the colony during chick-rearing, resulting in a high density of users per km². Thus, despite the expense of traveling further, individuals forage in oceanic areas with low primary productivity but with few users per km², which may increase capture success and reduce competition for prey (Weimerskirch 2007). Furthermore, red-billed tropicbirds have been reported to be mostly solitary at sea, exhibiting an opportunistic foraging pattern that often depends on predatory fish for prey availability and foraging over wide areas with very low densities to avoid intra- or interspecific feeding flocks (Spear and Ainley 2005). Extending travel time and distance to these areas may also increase the probability of finding high-quality prey, as these prey are usually scarce and less reliably caught (Shoji et al. 2015). In addition, the observed pattern of directionality of most Red-billed Tropicbird foraging trips towards the southwest of the islet could be influenced by wind patterns (southwest during the breeding season), resource distribution, or even by inter-colony segregation of foraging areas (Tarroux et al. 2016; Goto et al. 2017). However, future research is required to elucidate which factors and the extent to which they influence the directionality of foraging trips of breeding red-billed tropicbirds.

Relationship between bimodal foraging and parental care

The bimodal foraging strategy in seabirds is assumed to have evolved in response to the scarcity of resources near their colonies, with parents meeting their energetic requirements and those of their chicks, by using different foraging areas and increasing the size of those areas to reduce competition for prey (Welcker et al. 2012). This strategy evolved in pelagic foragers in response to prolonged parental care and

the constraints of central-place foraging (Ropert-Coudert et al. 2004). For red-billed tropicbirds, which have a breeding period of about 112–125 days until the fledgling leaves the nest (Castillo-Guerrero et al. 2011; Boeken 2016), this strategy seems to be an appropriate mechanism to deal with these constraints, especially at the beginning of the chick-rearing phase when the demands of altricial chicks are high (e.g., brooding, feeding, and protection) and must be met by their parents (Wittenberger and Tilson 1980; Dial 2003). Parental presence of red-billed tropicbirds from other colonies has been reported in ~82% and 10% of nests with small and large chicks, respectively (Nelson 2006). These findings are similar to our results, as the parents in our study exhibited a higher presence at the nest and a stable upward chick-feeding frequency during the ECR period than during the later rearing stages (Fig. 4a,b).

Based on what has been reported of the foraging behavior of Adélie penguins (*Pygoscelis adeliae*), there are two stages that parents must navigate during chick-rearing to deliver food to their chicks efficiently (Ropert-Coudert et al. 2004). The first stage comprises the beginning of brooding when the chicks are small, and parents frequently deliver food to maximize their food intake. If parents can maximize the rate at which energy is supplied to their chicks, the likelihood of reproductive success will increase. Conversely, when the sizes of the chicks and parents are the same, the travel time of foraging trips increases. Optimally, parents should alternate short trips and long trips, as this maximizes the rate at which they obtain food for themselves and, consequently, improves their future breeding fitness (Ropert-Coudert et al. 2004).

Meal sizes provided to the chicks

The results of this study suggest that the foraging ecology of red-billed tropicbirds is linked to their parental duties. The Red-billed Tropicbird adults of Peña Blanca seem to maximize food delivery to their chicks during the ECR stage by making both short and long trips. Young chicks, which lack the reserves to withstand prolonged periods of fasting, require regular parental provisioning during the first weeks after hatching, as this is a particularly critical stage for chick survival (Phillips and Hamer 1999). Once the Red-billed Tropicbird chicks nearly reach adult size at 5–6 weeks of age (Table S2), parents can spend more time foraging and less time at the nest (see Fig. 4a), as the lipid reserves of chicks allow them to tolerate longer periods of fasting, which the parents compensate for by increasing meal size (see Fig. 4c; Chaurand and Weimerskirch 1994), although larger meal sizes and food provisioning gradually decrease prior to fledgling when parents are unable or unwilling to maintain earlier levels of food provisioning (Riou and Hamer 2010; Riou et al. 2012; Arnold et al. 2016). This is

consistent with what has been reported for other seabirds in which high levels of coordination between mates regarding their foraging trips ensure a consistent supply of food for their chicks, although this coordination begins to decline as the chick-rearing period progresses (Tyson et al. 2017; Wojczulanis-Jakubas et al. 2018). However, these patterns can vary between species and even between conspecific individuals (Clutton-Brock 1991; McGraw et al. 2010; Royle et al. 2012).

On the other hand, studies of sooty shearwaters (*Ardenna grisea*) have shown that the parental decision to make either short or long trips after feeding chicks depends exclusively on the mass of the adult and not on other factors (e.g., chick nutritional status, duration of the previous trip, or endogenous rhythm), as birds always undertake long trips when their body mass falls below the threshold of 750 g (Weimerskirch 1998). Although we weighed the adults in this study, we did so only once when we retrieved the GPS devices. This prevented us from assessing whether adults undertook long trips when they reached a mass threshold, and we cannot rule out the involvement of parental body condition in foraging decisions or that factors influencing parental decisions to undertake long or short foraging trips may be species-specific (Baduini and Hyrenbach 2003). Further research employing a body condition index in red-billed tropicbirds could demonstrate the existence of a threshold value for this behavioral decision.

Bimodal foraging strategy could be controlled by different, but not mutually exclusive, factors to regulating parental investment in offspring (Granadeiro et al. 1998) or exclusively by adult body condition (Weimerskirch 1998). The extent to which each factor influences the foraging decisions of Red-billed Tropicbird parents is a key question that should be answered in future studies.

Conclusion

Based on the GPS data obtained from the foraging trips conducted by red-billed tropicbirds of Peña Blanca Islet, we can conclude that parents switched from a unimodal foraging strategy during the incubation stage to a bimodal foraging strategy once their chicks hatched. Parents undertook short and long foraging trips during the ECR period (chicks < 4 weeks old). Short trips were made to shallower areas (depths < 200 m) surrounding the breeding site with high Chl-a concentrations and low SST, whereas long foraging trips were made to deeper, less productive waters. The most plausible explanation for this bimodal strategy is that red-billed tropicbirds undertook long foraging trips to arrive in areas with low oceanic productivity that were undisputed by other birds and thus had low user density, thereby increasing the probability of finding high-quality prey by extending

their travel time and distance. Concurrently, parental presence at the nest was greater during the ECR period, which was associated with a higher rate of chick-feeding. The foraging strategy used by red-billed tropicbirds in this study is therefore clearly linked to parental duties. As young chicks require a high level of parental care at the nest and frequent feedings, parents alternated caring for their chicks. The parent on duty made short trips to provide for their chick without leaving it unattended for long periods, while its mate made long trips to feed itself. Adults then gradually reduced the time spent at the nest and increased the time spent foraging, compensating with larger meal sizes for their chicks as they grew. Our results seem to indicate that parental obligations trigger foraging decisions in red-billed tropicbirds during the chick-rearing period. The bimodal foraging strategy used by adults is a means to simultaneously meet their own high energetic demands and those of their young during the breeding season without sacrificing their own future breeding fitness.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-023-04375-1>.

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Author contributions Conceptualization: AP-O and JAC-G; Methodology: AP-O, JAC-G, PQ and PB; Fieldwork: AP-O, DAG-Z, SH-V and JAC-G; Formal analysis and investigation: AP-O, JAC-G, DAG-Z, JAP and EM; Writing—original draft preparation: AP-O and JAC-G; Writing—review and editing: AP-O, DAG-Z, JAP, SH-V, EM, PB, PQ and JAC-G; Funding acquisition: AP-O, SH-V and JAC-G; Resources: AP-O, PQ and JAC-G; Supervision: PQ and JAC-G.

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Data availability The data sets generated and analyzed during the current study are available in the OSF repository: https://osf.io/xw4ab/?view_only=deea243f23514f50bea27506c3407eab

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this work.

Ethics approval Fieldwork, including wildlife management and sampling, was conducted with the permission of the Dirección General de Vida Silvestre (DGVs, Mexico) under permits SGPA/DGVs/00404/15, SGPA/DGVs/01919/17, SGPA/DGVs/02779/21, and SPARN/DGVs/01482/22. All applicable institutional and/or national guidelines for the welfare and conservation of wildlife were followed. Individuals in this study were not handled for more than 10 min. The smallest amount of blood was collected from each animal. While the adults were sampled, we cared for their eggs and chicks until their parents returned to the nest. No adults abandoned their nests after capture. Further monitoring after this research allowed us to verify that the chicks were not abandoned by their parents after being handled for the purposes of this work.

Consent to participate N/A.

Consent to publish N/A.

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References

- Albano N, Masero JA, Sánchez-Guzmán JM, Villegas A, Santiago-Quesada F (2011) Effects of diet on growth-related patterns of energy and macronutrient assimilation efficiency in a semi-precocial bird, the Gull-billed Tern *Gelochelidon nilotica*. *Ardea* 99:93–101. <https://doi.org/10.5253/078.099.0111>
- Ambriz-Arreola I, Gómez-Gutiérrez J, Franco-Gordo MC, Lavaniegos BE, Godínez-Domínguez E (2012) Influence of coastal upwelling–downwelling variability on tropical euphausiid abundance and community structure in the inshore Mexican central Pacific. *Mar Ecol Prog Ser* 451:119–136. <https://doi.org/10.3354/meps09607>
- Arnold JM, Nisbet ICT, Oswald SA (2016) Energetic constraint of non-monotonic mass change during offspring growth: a general hypothesis and application of a new tool. *J Anim Ecol* 85:476–486. <https://doi.org/10.1111/1365-2656.12467>
- Austin RE, De Pascalis F, Arnould JPY, Haakonsson J, Votier SC, Ebanks-Petrie G, Austin T, Morgan G, Bennett G, Green JA (2019) A sex-influenced flexible foraging strategy in a tropical seabird, the magnificent frigatebird. *Mar Ecol Prog Ser* 611:203–214. <https://doi.org/10.3354/meps12859>
- Baduini CL, Hyrenbach KD (2003) Biogeography of Procellariiform foraging strategies: does ocean productivity influence provisioning? *Mar Ornithol* 31:101–112
- Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, Dai B, Grothendieck G (2015) lme4: linear mixed-effects models using “Eigen” and S4. R Package Version 1(1–10):1–98
- Beal M, Oppel S, Handley J, Pearmain EJ, Morera-Pujol V, Carneiro APB, Davies TE, Phillips RA, Taylor PR, Miller MGR, Franco AMA, Catry I, Patrício AR, Regalla A, Staniland I, Boyd C, Catry P, Dias MP (2021) track2KBA: An R package for identifying important sites for biodiversity from tracking data. *Methods Ecol Evol* 12:2372–2378. <https://doi.org/10.1111/2041-210X.13713>
- Bearhop S, Waldron S, Votier SC, Furness RW (2002) Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiol Biochem Zool* 75:451–458. <https://doi.org/10.1086/342800>
- Bennison A, Bearhop S, Bodey TW, Votier SC, Grecian WJ, Wakefield ED, Hamer KC, Jessopp M (2017) Search and foraging behaviors from movement data: A comparison of methods. *Ecol Evol* 8:13–24. <https://doi.org/10.1002/ece3.3593>
- Birt VL, Birt TP, Goulet D, Cairns DK, Montevecchi WA (1987) Ashmole's halo: direct evidence for prey depletion by a seabird. *Mar Ecol Prog Ser* 40:205–208
- Boeken M (2016) Breeding Success of Red-Billed Tropicbirds *Phaethon aethereus* on the Caribbean Island of Saba. *Ardea* 104:263–271. <https://doi.org/10.5253/arde.v104i3.a8>
- Campos LFAS, Andrade AB, Bertrand S, Efe MA (2018) Foraging behavior and at-sea distribution of White-Tailed Tropicbirds in tropical ocean. *Braz J Biol* 78:556–563. <https://doi.org/10.1590/1519-6984.173578>
- Capuzzo E, Lynam CP, Barry J, Stephens D, Forster RM, Greenwood N, McQuatters-Gollop A, Silva t, van Leeuwen SM, engelhard GH, (2017) A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. *Glob Chang Biol* 24:e352–e364. <https://doi.org/10.1111/gcb.13916>
- Castillo-Guerrero JA, Guevara-Medina MA, Mellink E (2011) Breeding ecology of the Red-billed tropicbird *Phaethon aethereus* under contrasting environmental conditions in the Gulf of California. *Ardea* 99:61–71. <https://doi.org/10.5253/078.099.0108>
- Chaurand T, Weimerskirch H (1994) The regular alternation of short and long foraging trips in the blue petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. *J Anim Ecol* 63:275–282. <https://doi.org/10.2307/5546>
- Cherel Y, Hobson KA, Hassani S (2005) Isotopic discrimination factors between food and blood and feathers of captive penguins: implications for dietary studies in the wild. *Physiol Biochem Zool* 78:106–115. <https://doi.org/10.1086/425202>
- Clarke JR (2001) Partitioning of foraging effort in Adélie penguins provisioning chicks at Béchervaise Island, Antarctica. *Polar Biol* 24:16–20. <https://doi.org/10.1007/s0030000000168>
- Clay TA, Oppel S, Lavers JL, Phillips RA, Brooke M-de L (2019) Divergent foraging strategies during incubation of an unusually wide-ranging seabird, the Murphy's petrel. *Mar Biol* 166:8. <https://doi.org/10.1007/s00227-018-3451-7>
- Clelland JB, Lea M-A, Hindell MA (2014) Use of the Southern Ocean by breeding Short-tailed shearwaters (*Puffinus tenuirostris*). *J Exp Mar Biol Ecol* 450:109–117. <https://doi.org/10.1016/j.jembe.2013.10.012>
- Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton, New Jersey
- Congdon BC, Krockenberger AK, Smithers BV (2005) Dual-foraging and co-ordinated provisioning in a tropical Procellariiform, the Wedge-tailed Shearwater. *Mar Ecol Prog Ser* 301:293–301. <https://doi.org/10.3354/meps301293>
- Crawley MJ (2007) The R book. Wiley, Chichester
- Dial KP (2003) Evolution of Avian Locomotion: Correlates of Flight Style, Locomotor Modules, Nesting Biology, Body Size,

- Development, and the Origin of Flapping Flight. *Auk* 120:941–952. [https://doi.org/10.1642/0004-8038\(2003\)120\[0941:EOALCO\]2.0.CO;2](https://doi.org/10.1642/0004-8038(2003)120[0941:EOALCO]2.0.CO;2)
- Diop N, Zango L, Beard A, Ba CT, Ndiaye PI, Henry L, Clingham E, Opper S, González-Solís J (2018) Foraging ecology of tropicbirds breeding in two contrasting marine environments in the tropical Atlantic. *Mar Ecol Prog Ser* 607:221–236. <https://doi.org/10.3354/meps12774>
- dos Santos I, Ramos JA, Ceia FR, Rodrigues I, Almeida N, Antunes S, Carreiro AR, Matos DM, Lopes RJ, Geraldes P, Paiva VH (2022) Sexual segregation in the foraging distribution, behaviour, and trophic niche of the endemic Boyd's shearwater (*Puffinus lherminieri boydi*). *Mar Biol* 169:144. <https://doi.org/10.1007/s00227-022-04127-7>
- Fieberg J, Kochanny CO (2005) Quantifying Home-Range Overlap: The Importance of the Utilization Distribution. *J Wildl Manage* 69:1346–1359. [https://doi.org/10.2193/0022-541X\(2005\)69\[1346:QHOTIO\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2)
- Franco-Gordo C, Godínez-Domínguez E, Suárez-Morales E, Freire J (2008) Interannual and seasonal variability of the diversity and structure of ichthyoplankton assemblages in the central Mexican Pacific. *Fish Oceanogr* 17:178–190. <https://doi.org/10.1111/j.1365-2419.2008.00463.x>
- Gitzen RA, Millsbaugh JJ, Kernohan BJ (2006) Bandwidth Selection for Fixed-Kernel Analysis of Animal Utilization Distributions. *J Wildl Manage* 70:1334–1344. [https://doi.org/10.2193/0022-541X\(2006\)70\[1334:BSFFAO\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2006)70[1334:BSFFAO]2.0.CO;2)
- González-Medina E, Castillo-Guerrero JA, Herzka SZ, Fernández G (2017) Flexibility in food resource allocation in parents and selectivity for offspring: variations in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values during breeding of the blue-footed booby. *Mar Biol* 164:38. <https://doi.org/10.1007/s00227-017-3070-8>
- Goto Y, Yoda K, Sato K (2017) Asymmetry hidden in birds' tracks reveals wind, heading, and orientation ability over the ocean. *Sci Adv* 3:e1700097. <https://doi.org/10.1126/sciadv.1700097>
- Granadeiro JP, Nunes M, Silva MC, Furness RW (1998) Flexible foraging strategy of Cory's shearwater, *Calonectris diomedea*, during the chick-rearing period. *Anim Behav* 56:1169–1176. <https://doi.org/10.1006/anbe.1998.0827>
- Hamer KC, Quillfeldt P, Masello JF, Fletcher K (2006) Sex differences in provisioning rules: responses of Manx shearwaters to supplementary chick feeding. *Behav Ecol* 17:132–137. <https://doi.org/10.1093/beheco/arj008>
- Harding AMA, Hobson KA, Wojciech W, Dmoch K, Karnovsky NJ, Van Pelt TI, Lifjeld JT (2008) Can stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) measurements of little auk (*Alle alle*) adults and chicks be used to track changes in high-Arctic marine foodwebs? *Polar Biol* 31:725–733. <https://doi.org/10.1007/s00300-008-0413-4>
- Harding A, Paredes R, Suryan R, Roby D, Irons D, Orben R, Renner H, Young R, Barger C, Dorresteijn I, Kitaysky A (2013) Does location really matter? An inter-colony comparison of seabirds breeding at varying distances from productive oceanographic features in the Bering Sea. *Deep-Sea Res II Top Stud Oceanogr* 94:178–191. <https://doi.org/10.1016/j.dsr2.2013.03.013>
- Hernández-Vázquez S, Castillo-Guerrero JA, Mellink E, Almaguer-Hernández AM (2018) Colony Size and Breeding Success of Red-billed Tropicbird (*Phaethon aethereus*) on Peña Blanca Island, Colima, México. *Waterbirds* 41:128–134. <https://doi.org/10.1675/063.041.0203>
- Hernández-Vázquez S, Mellink E, Castillo-Guerrero JA, Rodríguez-Estrella R, Hinojosa-Larios JA, Galván-Piña VH (2017) Ecología reproductiva del bobo café (*Sula leucogaster*) en tres islas del Pacífico tropical Mexicano. *Ornitol Neotrop* 28:57–66. <https://doi.org/10.58843/ornneo.v28i0.146>
- Hill T, Lewicki P (2007) STATISTICS: methods and applications. StatSoft, Tulsa, Oklahoma, USA.
- Jakubas D, Iliszko L, Wojczulanis-Jakubas K, Stempniewicz L (2012) Foraging by little auks in the distant marginal sea ice zone during the chick-rearing period. *Polar Biol* 35:73–81. <https://doi.org/10.1007/s00300-011-1034-x>
- Kono-Martínez T, Ortega-Ortiz CD, Olivos-Ortiz A, Torres-Orozco E, González-Rodríguez E (2017) Oceanographic conditions and marine mammals: identifying a potential relationship in the coastal region of the Mexican Central Pacific. *Rev Biol Mar Oceanogr* 52:479–494. <https://doi.org/10.4067/S0718-19572017000300006>
- Kozak ER, Franco-Gordo C, Godínez-Domínguez E, Suárez-Morales E, Ambriz-Arreola I (2020) Seasonal variability of stable isotope values and niche size in tropical calanoid copepods and zooplankton size fractions. *Mar Biol* 167:37. <https://doi.org/10.1007/s00227-020-3653-7>
- Le Corre M, Cherel Y, Lagarde F, Lormée H, Jouventin P (2003) Seasonal and inter-annual variation in the feeding ecology of a tropical oceanic seabird, the red-tailed tropicbird *Phaethon rubricauda*. *Mar Ecol Prog Ser* 255:289–301. <https://doi.org/10.3354/meps255289>
- Madden H, Satgé Y, Wilkinson B, Jodice PGR (2022) Foraging ecology of Red-billed Tropicbird *Phaethon aethereus* in the Caribbean during early chick rearing revealed by GPS tracking. *Mar Ornithol* 50:165–175
- Madden H, Boehm H, Mielke L (2023) Foraging Ecology of Red-Billed Tropicbirds on Saba, Caribbean Netherlands, During Early Chick-Rearing. *Ardea* 111:1–18. <https://doi.org/10.5253/arde.2022.a14>
- McGraw L, Székely T, Young LJ (2010) Pair bonds and parental behaviour. In: Székely T, Moore AJ, Komdeur J (eds) *Social behaviour: Genes, ecology and evolution*. Cambridge University Press, Cambridge, UK, pp 271–301
- Michelot T, Langrock R, Patterson TA (2016) moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models. *Methods Ecol Evol* 7:1308–1315. <https://doi.org/10.1111/2041-210X.12578>
- Micklem IA, Connan M, Stander N, McQuaid CD (2021) Influence of ontogeny on stable isotope ratios and trophic discrimination factors of African penguin (*Spheniscus demersus*) tissues. *Mar Biol* 168:96. <https://doi.org/10.1007/s00227-021-03877-0>
- Nelson JB (2006) Pelicans, cormorants, and their relatives, the Pelecaniformes. Oxford University Press, New York, USA
- Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn JD, Mitchell RD, Stairs GR (eds) *Analysis of Ecological Systems*. Ohio State University Press, Columbus, Ohio, USA, pp 154–177
- Phillips RA, Hamer KC (1999) Lipid reserves, fasting capability and the evolution of nestling obesity in procellariiform seabirds. *Proc R Soc B Biol Sci* 266:1329–1334. <https://doi.org/10.1098/rspb.1999.0783>
- Phillips JA, Hurlford T, Fayet AL (2023) How do resource distribution and taxonomy affect the use of dual foraging in seabirds? A review. *Behav Ecol* 34:769–779. <https://doi.org/10.1093/beheco/arak052>
- Piña-Ortiz A, Castillo-Guerrero JA, Enríquez-Paredes LM, Fernández G, Hernández-Vázquez S, Quillfeldt P (2023) Body size variation in a tropical seabird along a latitude-productivity gradient. *J Ornithol* 164:327–339. <https://doi.org/10.1007/s10336-022-02037-5>
- QGIS.org, 2020. QGIS Geographic Information System. QGIS Association. <http://www.qgis.org>
- Quillfeldt P (2002) Begging in the absence of sibling competition in Wilson's storm-petrels, *Oceanites oceanicus*. *Anim Behav* 64:579–587. <https://doi.org/10.1006/anbe.2002.3090>
- R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

- Riou S, Hamer KC (2010) Lipid metabolism, begging behaviour and nestling obesity in a pelagic seabird. *Funct Ecol* 24:340–346. <https://doi.org/10.1111/j.1365-2435.2009.01651.x>
- Riou S, Chastel O, Hamer KC (2012) Parent–offspring conflict during the transition to independence in a pelagic seabird. *Behav Ecol* 23:1102–1107. <https://doi.org/10.1093/beheco/ars079>
- Ropert-Coudert Y, Wilson RP, Daunt F, Kato A (2004) Patterns of energy acquisition by a central place forager: benefits of alternating short and long foraging trips. *Behav Ecol* 15:824–830. <https://doi.org/10.1093/beheco/arih086>
- Royle N, Smiseth P, Kölliker M (2012) The evolution of parental care. Oxford University Press, Oxford, UK
- RStudio Team (2023) RStudio: integrated development for R. RStudio, PBC, Boston, MA
- Salas J, Gomis D, Olivios-Ortiz A, García-Urbe G (2006) Seasonal hydrodynamical features on the shelf of Colima (west coast of Mexico). *Sci Mar* 70:719–726. <https://doi.org/10.3989/scimar.2006.70n4>
- Saraux C, Robinson-Laverick SM, Le Maho Y, Ropert-Coudert Y, Chiaradia A (2011) Plasticity in foraging strategies of inshore birds: how Little Penguins maintain body reserves while feeding offspring. *Ecology* 92:1909–1916. <https://doi.org/10.1890/11-0407.1>
- Sears J, Hatch SA, O'Brien DM (2009) Disentangling effects of growth and nutritional status on seabirds stable isotope ratios. *Oecologia* 159:41–48. <https://doi.org/10.1007/s00442-008-1199-3>
- Shoji A, Aris-Brosou S, Fayet A, Padgett O, Perrins C, Guilford T (2015) Dual foraging and pair coordination during chick provisioning by Manx shearwaters: empirical evidence supported by a simple model. *J Exp Biol* 218:2116–2123. <https://doi.org/10.1242/jeb.120626>
- Signer J, Fieberg J, Avgar T (2019) Animal movement tools (amt): R package for managing tracking data conducting habitat selection analyses. *Ecol Evol* 9:880–890. <https://doi.org/10.1002/ece3.4823>
- Sommerfeld J, Hennenke JC (2010) Comparison of trip duration, activity pattern and diving behaviour by Red-tailed Tropicbirds (*Phaethon rubricauda*) during incubation and chick-rearing. *Emu* 110:78–86. <https://doi.org/10.1071/MU09053>
- Spear LB, Ainley DG (2005) At-sea distributions and abundance of tropicbirds in the eastern Pacific. *Ibis* 147:353–366. <https://doi.org/10.1111/j.1474-919x.2005.00411.x>
- Steen H, Vogedes D, Broms F, Falk-Petersen S, Berge J (2007) Little auks (*Alle alle*) breeding in a High Arctic fjord system: bimodal foraging strategies as a response to poor food quality? *Polar Res* 26:118–125. <https://doi.org/10.1111/j.1751-8369.2007.00022.x>
- Suryan RM, Irons DB, Benson J (2000) Prey switching and variable foraging strategies of Black-Legged Kittiwakes and the effect on reproductive success. *The Condor* 102:374–384. [https://doi.org/10.1650/0010-5422\(2000\)102\[0374:PSAVFS\]2.0.CO;2](https://doi.org/10.1650/0010-5422(2000)102[0374:PSAVFS]2.0.CO;2)
- Tarroux A, Weimerskirch H, Wang S-H, Bromwich DH, Chérel Y, Kato A, Ropert-Coudert Y, Varpe Ø, Yoccoz NG, Descamps S (2016) Flexible flight response to challenging wind conditions in a commuting Antarctic seabird: do you catch the drift? *Anim Behav* 113:99–112. <https://doi.org/10.1016/j.anbehav.2015.12.021>
- Tyson C, Kirk H, Fayet A, Van Loon EE, Shoji A, Dean B, Perrins C, Freeman R, Guilford T (2017) Coordinated provisioning in a dual-foraging pelagic seabird. *Anim Behav* 132:73–79. <https://doi.org/10.1016/j.anbehav.2017.07.022>
- Vandenabeele SP, Shepard EL, Grogan A, Wilson RP (2012) When three per cent may not be three per cent; device-equipped seabirds experience variable fight constraints. *Mar Biol* 159:1–14. <https://doi.org/10.1007/s00227-011-1784-6>
- Wand MP, Jones MC (1994) Kernel Smoothing. Chapman and Hall/CRC, New York, USA
- Weber SM, Richardson AJ, Brown J, Bolton M, Clark BL, Godley BJ, Leat E, Oppel S, Shearer L, Soetaert KER, Weber N, Broderick AC (2021) Direct evidence of a prey depletion “halo” surrounding a pelagic predator colony. *PNAS* 118:e2101325118. <https://doi.org/10.1073/pnas.2101325118>
- Weimerskirch H (1998) How can a pelagic seabird provision its chick when relying on a distant resource? Cyclic attendance, foraging decision and body condition in sooty shearwaters. *J Anim Ecol* 67:99–109. <https://doi.org/10.1046/j.1365-2656.1998.00180.x>
- Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Res Part II Top Stud Oceanogr* 54:211–223. <https://doi.org/10.1016/j.dsr2.2006.11.013>
- Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P (1993) Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk* 110:325–342. <https://doi.org/10.1093/auk/110.2.325>
- Weimerskirch H, Chastel O, Ackermann L, Chaurand T, Cuenot-Chaillet F, Hindermeyer X, Judas J (1994) Alternate long and short foraging trips in pelagic seabird parents. *Anim Behav* 47:472–476. <https://doi.org/10.1006/anbe.1994.1065>
- Weimerskirch H, Ancel A, Caloin M, Zahariev A, Spaggiari J, Kersten M, Chastel O (2003) Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. *J Anim Ecol* 72:500–508. <https://doi.org/10.1046/j.1365-2656.2002.00720.x>
- Welcker J, Harding AMA, Karnovsky NJ, Steen H, Strøm H, Gabrielsen GW (2009) Flexibility in the bimodal foraging strategy of a high Arctic alcid, the little auk *Alle alle*. *J Avian Biol* 40:388–399. <https://doi.org/10.1111/j.1600-048X.2008.04620.x>
- Welcker J, Beiersdorf A, Varpe Ø, Steen H (2012) Mass fluctuations suggest different functions of bimodal foraging trips in a central-place forager. *Behav Ecol* 23:1372–1378. <https://doi.org/10.1093/beheco/ars131>
- Wilson RP, McMahon CR (2006) Measuring devices on wild animals: what constitutes acceptable practice? *Front Ecol Environ* 4:147–154. [https://doi.org/10.1890/1540-9295\(2006\)004\[0147:MDOWAW\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2006)004[0147:MDOWAW]2.0.CO;2)
- Wittenberger JF, Tilson RL (1980) The evolution of monogamy: hypotheses and evidences. *Annu Rev Ecol Evol Syst* 11:197–232. <https://doi.org/10.1146/annurev.es.11.110180.001213>
- Wojczulanis-Jakubas K, Araya-Salas M, Jakubas D (2018) Seabird parents provision their chick in a coordinated manner. *PLoS ONE* 13:e0189969. <https://doi.org/10.1371/journal.pone.0189969>
- Wood AG, Naef-Daenzer B, Prince PA, Croxall JP (2000) Quantifying habitat use in satellite-tracked pelagic seabirds: application of kernel estimation to albatross locations. *J Avian Biol* 31:278–286. <https://doi.org/10.1034/j.1600-048X.2000.310302.x>

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