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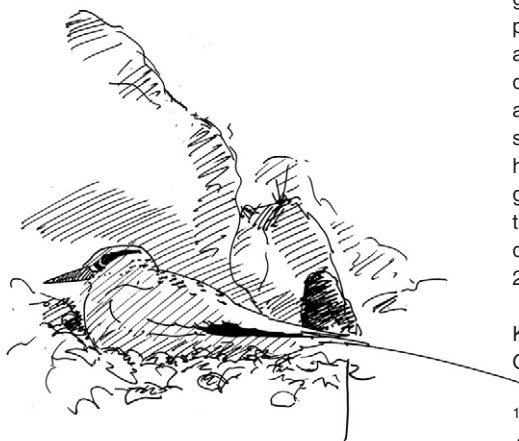
Breeding ecology of the Red-billed Tropicbird *Phaethon aethereus* under contrasting environmental conditions in the Gulf of California

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We studied the breeding ecology of Red-billed Tropicbirds *Phaethon aethereus* at Farallón de San Ignacio, Sinaloa, in the south-central part of the Gulf of California, during two years with different oceanographic conditions: 2004, a neutral year, and 2007, a moderate El Niño year. We characterized oceanic changes by sea surface temperature and chlorophyll *a* concentration (150 km around the colony) from monthly satellite images. During two 5-day visits every month from January to May of each year we recorded timing of breeding, parental attendance, chick diet, and maximum diving depth of adults. We analyzed hatching and fledging success, chick growth and body condition. In agreement with oceanographic differences, we expected differences in timing of breeding, diet and foraging behaviour and lower breeding success and chick growth in the El Niño year. Sea surface temperature was higher, and chlorophyll concentration lower during early 2007 than in 2004. Average laying date and peak of laying occurred later in 2004 than in 2007. In 2007 adults dived deeper (2.09 ± 0.96 vs. 0.96 ± 0.66 m), had a different and more varied diet, and spent more time at sea at the expense of nest attendance than in 2004, suggesting that less food was available for this species in 2007. In agreement, hatching success was lower (35 vs. 75%), and chicks were lighter (641 vs. 739 g) and in worse body condition in 2007. Overall, despite the lower body condition of the chicks, the species seemed to exhibit some capacity to cope with the different conditions derived from warmer waters during the mild El Niño of 2006–2007.



Key words: breeding ecology, environmental fluctuation, El Niño Southern Oscillation, chick growth, Sinaloa, Mexico

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In tropical areas, seasonal changes in the marine environment, like monsoons or seasonal upwelling can occur, and although seasonality in food availability is less marked than at higher latitudes, it does influence seabird breeding cycles and breeding ecology (Harrison *et al.* 1983, Morris & Chardine 1992, Le Corre 2001, Le Corre *et al.* 2003, Jaquemet *et al.* 2007, Weimerskirch 2007, Catry *et al.* 2009). Seabirds in the tropics can also face variability in physical and trophic conditions

between years due to anomalies such as the El Niño Southern Oscillation (ENSO). Seabirds have to cope with these inter-annual changes, for instance by changing their foraging areas and diets, but very bad conditions may lead to adults dying and partial or complete reproductive failures (e.g. Schreiber & Schreiber 1984, Valle *et al.* 1987, Anderson 1989, Cruz & Cruz 1990, Ramos *et al.* 2004). However, whether a given species is able to cope (to survive and reproduce), is likely to

depend on the magnitude of the variations and on intrinsic factors, such as species or population specific foraging habits. Pelagic species and those that have short foraging ranges and/or are little able to change their diet are more vulnerable to environmental changes than species with large foraging areas and a less specialized diet (Devney *et al.* 2009, Catry *et al.* 2009). Even within a given species, different sex/age groups can be affected in different ways by inter-annual variability, especially in recruitment and survival (Oro *et al.* 2010). Thus, long-lived tropical seabirds may have to cope with seasonal and inter-annual variation in environmental conditions.

Understanding the adaptations of seabirds to the unpredictability of their food resources is a central theme in seabird ecology (Ashmole 1971, Ramos *et al.* 2002, Weimerskirch 2007), especially in tropical oceans where productivity is lower, prey more patchily distributed, and food resources show less seasonal variation than in temperate or polar environments (Weimerskirch 2007). Knowledge of the breeding ecology of tropical seabirds under different environmental conditions is still necessary to clarify the topic. In addition, in the context of climatic change it is of interest to study the response of different species and populations to changes in their environment, to determine their vulnerability to local and regional inter-annual changes in the ocean (Monticelli *et al.* 2007).

In this study, we characterized the breeding biology of a tropical seabird, the Red-billed Tropicbird *Phaethon aethereus*, at a colony in the southern Gulf of California, Mexico, a region where the species' ecology is not well known, and that exhibits seasonal and inter-annual environmental fluctuations in its physical properties derived mainly from seasonal upwelling and ENSO cycles (Soto-Mardones *et al.* 1999).

Red-billed Tropicbirds are found in the tropical zones of the Pacific and Atlantic Oceans, and in the north of the Indian Ocean (Orta 1992). Despite their wide distribution, the world population of Red-billed Tropicbirds is small, estimated to be less than 8000 pairs (Lee & Walsh-McGehee 2000), including about 4900 breeding pairs in the Pacific (Spear & Ainley 2005a). In the Pacific Ocean, tropicbirds nest on rocky islands along the coast of the Americas, from the northern Gulf of California and Revillagigedo Islands to the Galápagos Islands and, possibly, Plata Island, Ecuador (Spear & Ainley 2005a,b).

Both at Ascension Island in the Atlantic Ocean and at the Galápagos Islands in the Pacific, Red-billed Tropicbirds breed throughout the year, with peaks in some months and a breeding cycle of about 11 months

(Stonehouse 1962, Snow 1965, Harris 1969). They lay only one egg that is incubated for 42 days, and chicks fledge at between 12 and 15 weeks. Documented breeding success has been 32–55% at Galapagos and 51% at Ascension, but these studies were carried out under El Niño conditions (Stonehouse 1962, Snow 1965, Harris 1969). Other studies of this species were limited to an estimate of their numbers and habitat use in the Pacific Ocean (Spear & Ainley 2005a, b), and some local counts and anecdotal reports (e.g. González-Bernal *et al.* 2002, Mellink & Riojas-López 2005).

In Mexico, Red-billed Tropicbirds are considered threatened (SEMARNAT 2002). Along the Pacific coast of Mexico, colonies occur at least as far south as Guerrero (Mellink & Riojas-López 2005), and the population in the Gulf of California has been estimated at 500–1000 pairs (Everett & Anderson 1991). The colony at Farallón de San Ignacio, with up to 250 pairs, is one of the two largest known colonies in the Gulf of California (Guevara-Medina *et al.* 2008).

We studied the breeding ecology of Red-billed Tropicbirds at Farallón de San Ignacio Island, a region with seasonal upwelling in the Gulf of California, during two years with different oceanographic conditions: 2004, considered a neutral year, and 2007, a moderate El Niño year. Our objectives were to determine how feeding conditions, feeding behaviour and reproduction differed between the two years. We expected that Red-billed Tropicbirds should exhibit (1) delayed laying and a shorter breeding season, (2) change in their diet and foraging behaviour, (3) lower hatching and fledging success, and (4) lower chick growth in 2007 compared to 2004.

METHODS

Study area

Farallón de San Ignacio (25°26'N, 109°22'W) is located 36 km off the coast in northern Sinaloa (Fig. 1). The island rises 140 m above sea level. Its base encompasses about 16 ha and its top approximately 3.5–4 ha, and is nearly flat (González-Bernal *et al.* 2002). The island is surrounded by water 200–500 m deep immediately offshore. In addition to Red-billed Tropicbirds, Brown and Blue-footed boobies *Sula leucogaster* and *S. nebouxii*, Double-crested Cormorants *Phalacrocorax auritus*, and Heermann's Gulls *Larus heermanni* nest on the island (González-Bernal *et al.* 2002, Guevara-Medina *et al.* 2008).

The climate of the region is warm and dry, with a mean annual temperature of 25°C (10.5°C in January,

and over 36°C in July), and 300 mm of rain that falls in the summer (June–September) and early autumn (October; INEGI 2007). The area has a clear seasonal oceanographic pattern, with warm Equatorial Surface Waters during the summer (July–September), and wind-driven upwelling of Pacific Subsurface Waters during the winter (December–March), causing the lowering of sea surface temperatures by about 10°C (Soto-Mardones *et al.* 1999). During summer, the concentration of photosynthetic pigments is low, whereas in winter, when northerly winds produce local upwelling, productivity is high (Alvarez–Borrego 2002).

During the 2004 breeding season (beginning in late 2003) sea surface temperature anomalies were close to 0 and this year was considered an ENSO-neutral year. In contrast, during the 2007 breeding season, sea surface temperature anomalies in the Pacific exceeded 1°C, which represent moderate El Niño conditions. This event lasted from late 2006 to March 2007 and, afterwards, conditions returned to ENSO-neutral (http://www.cpc.ncep.noaa.gov/products/expert_assessment/ENSO_DD_archive.shtml). El Niño conditions are characterized by a positive Oceanic Niño Index (ONI) greater than or equal to +0.5°C and persisting for three consecutive months. The ONI is based on sea surface temperature departures from average in the Niño 3.4 region (equatorial central Pacific), and is a principal measure for monitoring, assessing, and predicting ENSO. The maximum historical ONI value is 2.5 (in 1998), whereas it was 1.1 in 2007 (NOAA 2009).

Oceanographic conditions and timing of the breeding season

To characterize oceanographic conditions, we used monthly Sea Surface Temperature (°C) and chlorophyll *a* concentrations (mg/m³). We derived sea surface temperature and chlorophyll data between coordinates 25.60° N, 110.45° W and 24.7° N, 109.45° W (150 km around the colony; Fig. 1), with 4 × 4 km and 5.5 × 5.5 km resolution, respectively, from data recorded by the aqua-MODIS satellite (<http://oceancolor.gsfc.nasa.gov>).

We made two 5-day visits per month to the island from January to May in 2004 and 2007. We searched for nests in all accessible parts of the island. For each nest, we obtained height above sea level, depth, width of the nest entrance, and orientation (N, E, S, W, NE, SE, SW, or NW). We measured burrow characteristics because in many seabird species these affect the parents' ability to protect the eggs and chicks from predators and thermal stress. We monitored all nests found throughout the season (46 in 2004, and 55 in

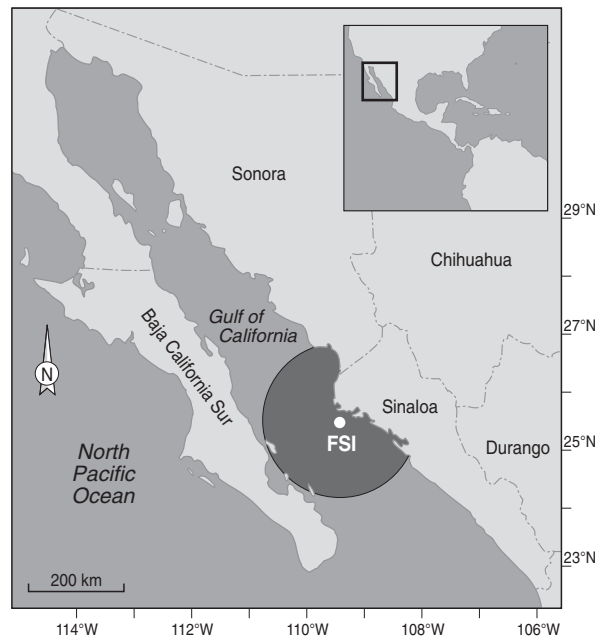


Figure 1. Geographic location of the study area: Farallón de San Ignacio Island (FSI), south-central Gulf of California, Mexico. Shading represents the area from which monthly sea surface temperature and chlorophyll concentration were calculated.

2007). We marked all eggs with waterproof ink to note if they were replaced. Chicks were colour-coded individually with plastic tarsal bands. The onset of the breeding season was determined by subtracting 42 days (mean incubation time, Stonehouse 1962, Snow 1965, Harris 1969) from the date the earliest chicks hatched. If any nests failed during November and December, they were not detected. However, we visited the island in August and October 2004 and observed no breeding activity, so the likelihood that we missed asynchronously early nests was probably small.

Parental attendance, foraging behaviour and diet

We used the proportion of times that parents were present at nests (two daily checks, one in the morning and one in the afternoon) throughout incubation and during the first three weeks after hatching as an index of parental presence.

The maximum diving depth of adult tropicbirds was determined using capillary tubes (0.8 mm internal diameter, 15 cm long, internally covered with icing sugar, and sealed at one end; Burger & Wilson 1988), attached to one of the central rectrices with water-proof tape. We attached these to adults with chicks less than 3 weeks old during January and February in 2004 and

2007. Tubes were recovered an average of 38.4 ± 11.9 (SD) hrs after being deployed, when adults returned from foraging trips. Burger & Wilson (1988) tested the accuracy and applicability of this method and determined that differences between real and estimated depths averaged $<3\%$ in single immersions to any depth up to 140 m. With multiple immersions, errors were usually $<10\%$ and always $<25\%$. The main disadvantages of the method are that only maximum diving depth is recorded and that high environmental humidity makes reading the tubes difficult. We recovered 35 capillary tubes (23 in 2004 and 12 in 2007) with clearly readable immersion marks.

To characterize diet, we examined 24 regurgitations each year obtained mainly from chicks when handled or from adults trying to feed chicks. Prey items were identified with the aid of Fischer *et al.* (1995), and those that were complete were measured (total length and weight). All mass regurgitated was given back to the chick, to reduce adverse effects on chick growth and body condition.

Breeding success and chick growth

During each year, breeding success was assessed as hatching success (eggs hatched / eggs laid) and fledging success (chicks reaching flight / hatched eggs). We monitored the growth of 36 chicks in 2004 and 31 chicks in 2007 by daily measuring their culmen and tarsus with callipers (± 0.1 mm) and their mass with a digital balance (± 1 g). Using chicks of known age (seven in 2004 and eight in 2007), we estimated the age of those that hatched between visits (always smaller than 8-day periods).

Body condition of chicks was calculated from measurements of body mass, by correcting for body size. Body mass was regressed upon a body size index (PC1 from culmen and ulna measures, 97% of variance explained) and the residual, expressed as a proportion of the predicted value, was used as an index of body condition (Hamer & Hill 1993). Since we had multiple measurements for each chick, we calculated their average body condition.

Statistical analyses

Average laying date (days after 1 October) was compared between years using a General Linear Model (GLM) considering an identity-link and normal distribution. We compared the percent of parental presence during incubation and during post-hatching in 2004 and 2007 with a normal-identity link GLM. Year was used as a categorical factor and laying date was included as covariate. Maximum diving depths were

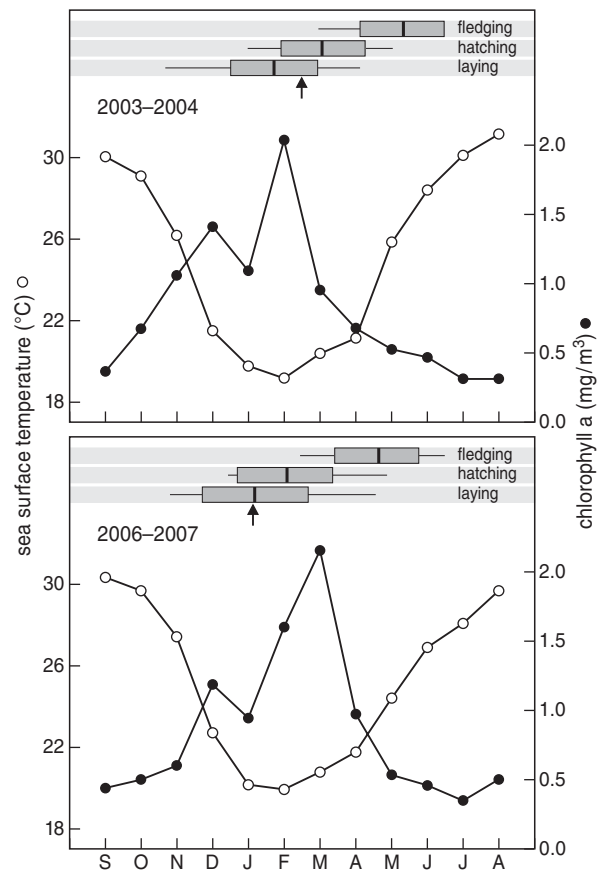


Figure 2. Timing of the breeding season, sea surface temperatures ($^{\circ}\text{C}$) and chlorophyll *a* concentrations (mg/m^3) during an El Niño-neutral year (2003–2004) and a moderate El Niño year (2006–2007). The three horizontal bars on top of each panel show the mean \pm SD (box) and range (lines) of the timing of breeding: egg-laying; hatching of eggs; fledging of chicks, see Table 1 for details and statistical tests). Peaks of laying are indicated by the arrows.

compared between years with the same model, but we used year and reproductive stage (incubation or brooding) as categorical factors, and date (days since 1 October) as a covariate.

To compare diet composition between the two years we applied the non-parametric analysis of similarity (ANOSIM), using PRIMER statistical software (version 5.2.9). The data on regurgitates were grouped in four categories (flying fish, other fishes, cephalopods and crustaceans) and the number of prey in each group present within each sample was converted to percentage. A similarity matrix using the Bray–Curtis measure was generated. ANOSIM tests were run on the matrices using 999 permutations to test for statistically significant differences in diet composition between samples.

In addition, we predicted the amount of prey species in each year through the relation between sampling effort and the prey species accumulation curve. To build this accumulation curve we resampled the data through ($n = 100$) using EstimateS, Ver. 8.0 (Colwell 2006). Afterwards we adjusted the model: prey-species = $(a \times \text{no. samples}) / (1 + (b \times \text{no. samples}))$ using Statistica 7.1 (StatSoft 2005) and predicted richness as a function of a and b from the equation of the curve (Jiménez-Valverde & Hortal 2003).

To compare hatching and fledging success we used a logit-link GLM due to the binomial distribution of the response variable. First, we used a model containing only year effects for both hatching and fledging success; then we added percent of parental attendance during the corresponding period (incubation, chick tending), and laying date as continuous predictors in both models. All the nest characteristics were removed because they did not significantly influence the response variables in preliminary analyses.

Culmen length at fledging (70–80 days) and maximum mass (60–70 days) were analyzed through identity-link GLM, with year (2004 or 2007) as a categorical factor, and laying date as a continuous predictor. Average body condition was analyzed in a similar way, but adding survival (survived, died) as an additional categorical factor.

RESULTS

Timing of the breeding season

Mean sea surface temperature during the 2004 and 2007 breeding season (October–May) was 22.9°C and 23.4°C respectively. At the beginning and middle of the breeding season (October–April), sea surface temperature was lower in 2004 than 2007, with a maximum difference of 1.2–1.3°C in November and December (Fig. 2) and, at the end of breeding season (May–June), warmer in 2004 than in 2007 (Fig. 2). Chlorophyll concentration exhibited the inverse pattern, with maximum values in February and March. In the first half of the breeding season (October–February), chlorophyll concentration was higher in 2004 than in 2007, but from March to April it was higher in 2007. The maximum peak of chlorophyll concentration was shifted one month between years (Fig. 2).

Red-billed Tropicbirds nested at Farallón de San Ignacio from late October through early June in 2004 and 2007 (Fig. 2). In both years, the onset of the breeding season coincided with the time at which the sea surface temperature dropped below 26–27°C (Fig. 2). The first documented egg was laid on 21 and 28 October, respectively. Average laying date and peak of laying occurred later in 2004 than in 2007 (Fig. 2, Table 1).

Table 1. Pairwise comparisons of 2004 vs. 2007 (means \pm SE, sample sizes in brackets) in the timing of the breeding season, breeder foraging behaviour and breeding parameters of Red-billed Tropicbirds at Farallón de San Ignacio, Mexico. Statistical tests: $df = 1$ in each case, except for Diet composition and Predicted number of prey species (see text for more details).

Parameter	2004	2007	Statistical test
Laying date (days since 1 October)	113 \pm 5.2 (49)	97 \pm 5.5 (62)	$\chi^2 = 4.4, P = 0.035$
Parental attendance during incubation (%)	88 \pm 3.1 (36)	68 \pm 3.4 (40)	$\chi^2 = 10.3, P = 0.001$
Parental attendance post-hatching (%)	75 \pm 5.2 (24)	58 \pm 5.4 (21)	$\chi^2 = 3.1, P = 0.08$
Maximum diving depth (m) of adults	0.96 \pm 0.14 (23)	2.09 \pm 0.27 (12)	$\chi^2 = 26, P < 0.001$
Diet composition (%):	(24)	(24)	$R = 0.084, P = 0.025$
Flyingfish	40 \pm 8.7	37.5 \pm 10.1	
Other fishes	13 \pm 6.8	43.7 \pm 10.1	
Squid	40 \pm 8.96	14.6 \pm 7.0	
Pelagic red crab	7 \pm 4.4	4.2 \pm 4.2	
Predicted number of prey species	11 \pm 1.4 (24)	24 \pm 1.4(24)	$a = 1.05, b = 0.09, r^2 = 0.98$ $a = 0.96, b = 0.04, r^2 = 0.99$
Hatching success (%)	75 \pm 7.3 (36)	35 \pm 7.6 (40)	$\chi^2 = 11.43, P < 0.001$
Fledging success (%)	78 \pm 6.8 (36)	77 \pm 7.2 (36)	$\chi^2 = 0.016, P = 0.89$
Culmen length at fledging (mm)	51.56 \pm 0.37 (25)	50.51 \pm 0.57 (23)	$\chi^2 = 2.08, P = 0.15$
Maximum mass (g) attained by chicks	724 \pm 10.5 (25)	600 \pm 21.8 (23)	$\chi^2 = 22.3, P < 0.001$
Chick body condition	0.11 \pm 0.028 (25)	-0.12 \pm 0.020 (23)	$\chi^2 = 51.5, P < 0.001$

Parental attendance, foraging behaviour and diet

Parental nest attendance during incubation was lower in 2007 than in 2004 (Fig. 3A, Table 1), and post-hatching parental attendance was also lower in 2007 than in 2004, but not significantly so (Fig. 3A, Table 1). Adult tropicbirds dived significantly shallower in 2004 than in 2007 (Fig. 3B, Table 1). In 2004 and 2007, adults delivered 8 and 12 different species of prey to their chicks, respectively, but the two main prey species (Sharpchin Flyingfish *Fodiator acutus rostratus* and Dart Squid *Loliolopsis diomedae*) were the same (Appendix 1). According to the prey species / sampling effort curve (see Methods), there were 11 prey species in 2004 and 24 in 2007 (Table 1). ANOSIM tests revealed slight but significant differences in diet composition

between 2004 and 2007 (Table 1). This difference was due to an increase in the amount of fish with a corresponding decrease in the importance of squid during the 2007 breeding season (Fig. 3C).

Reproduction and chick growth

All clutches ($n = 101$) consisted of one egg. Hatching success was significantly higher in 2004 than in 2007 (Fig. 4A, Table 1), whereas fledging success did not differ between the years (Fig. 4B, Table 1). When parental attendance was added to the model containing only year effects and laying date, both hatching success (Wald $\chi^2 = 14.2$, $df = 1$, $P < 0.001$) and fledging success (Wald $\chi^2 = 6.97$, $df = 1$, $P = 0.008$) were explained entirely by parental attendance, whereas

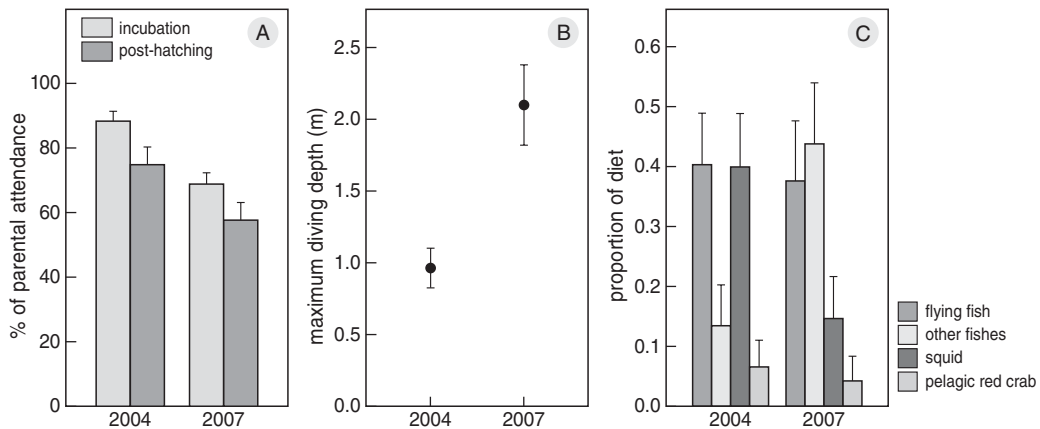


Figure 3. (A) Parental attendance during incubation (%), mean \pm SE) and post-hatching, (B) maximum diving depth (m, mean \pm SE), and (C) diet contribution (proportion, mean \pm SE) of flying fish, other fishes, squid and pelagic red crab during an El Niño-neutral year (2004) and a moderate El Niño year (2007). See Table 1 for details and statistical tests.

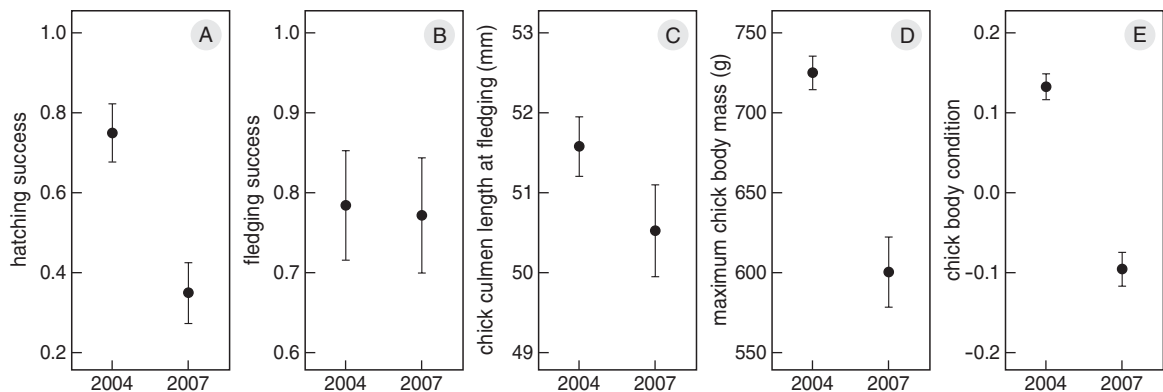


Figure 4. Breeding performance during an El Niño-neutral year (2004) and a moderate El Niño year (2007, means \pm SE): (A) hatching success, (B) fledging success, (C) culmen length of chicks at fledging, (D) maximum body mass of fledged chicks, and (E) body condition of fledged chicks. See Table 1 for details and statistical tests.

year was no longer significant for hatching success (Wald $\chi^2 = 2.14$, $df = 1$, $P = 0.14$) and fledging success (Wald $\chi^2 = 1.88$, $df = 1$, $P = 0.17$).

During both years, chicks fledged at 83 days after hatching (± 7.8 in 2004, $n = 19$, and ± 10.4 in 2007, $n = 22$) and did not differ in culmen length at fledging (Fig. 4C, Table 1). However, in 2004 the maximum body mass attained by chicks was higher in 2004 compared to 2007 (Fig. 4D, Table 1). Also, chicks that fledged in 2004 were in better body condition than those in 2007 (Fig. 4E, Table 1). In both years, chicks that died were in poorer condition than those that fledged (Wald $\chi^2 = 10.5$, $df = 1$, $P = 0.001$).

DISCUSSION

We studied the breeding biology of red-billed tropicbirds by comparing two different years: a normal year (2004) and a moderate El Niño year (2007). Timing of the breeding season, feeding conditions, and parental attendance between these two years differed markedly, probably primed by differences in sea surface temperature (lower in 2004 than in 2007), and accordingly differences in patterns of primary productivity (sea water chlorophyll content was higher in the pre-breeding and early breeding season in 2004 than in 2007). Inter-annual changes in feeding conditions and parental attendance suggested better conditions in 2004 than in 2007, and accordingly breeding success, chick growth, and chick body condition were higher during 2004 than in 2007.

Timing of the breeding season

The breeding of Red-billed Tropicbirds at Farallón de San Ignacio in our study was markedly seasonal, beginning in November and continuing until early June when the last fledglings left their nests. This seasonality coincides with the annual pattern of low summer (June–August) to high winter (December–February) productivity that characterizes the east margin of the Gulf of California (Alvarez-Borrego 2002). The relatively rapid decrease in sea surface temperature (change of trend) before the onset of reproduction indicates a strong modification of the environment, which preceded the increase in marine productivity. Other tropical seabird species in the Indian Ocean, such as Sooty Tern, Red-footed Booby, Audubon's Shearwater and Red-tailed Tropicbird, exhibit seasonal patterns when they inhabit areas that have seasonal, and predictable, changes in their physical conditions (mostly indicated by sea surface temperature; Le Corre 2001, Jaquem

et al. 2007). Hermann's Gull, Elegant Tern (Velarde *et al.* 2004), and Blue-footed Booby (J.A. Castillo-Guerrero, unpubl. data) colonies in the Gulf of California have a seasonal breeding season related to the upwelling season, when the abundance of small pelagic fishes increases. So the Red-billed Tropicbird colony in our study contrasts with colonies at Isla Ascension in the south Atlantic (Stonehouse 1962) and Isla Daphne, Islas Galapagos (Snow 1965, Harris 1969), which lack clear oceanographic seasonality, and exhibit breeding throughout the year.

In some marine birds, the onset of egg-laying has been linked to sea surface temperature (Diamond 2003, Jaquem *et al.* 2007, Tomita *et al.* 2009), probably because of its direct and indirect effects on food availability (Vlietstra *et al.* 2005, Frederiksen *et al.* 2006, Tomita *et al.* 2009). In tropical areas, surface enrichment in chlorophyll leads to a higher abundance of zooplankton and fish (Piontkovski & Williams 1995), which are largely preyed on by tropical seabirds. Red-tailed Tropicbirds (*P. rubricauda*) nesting on Aldabra and Europa Islands in the Western Indian Ocean bred seasonally in austral summer when sea surface temperature increased above 27°C (Prys-Jones & Peet 1980, Le Corre 2001). At Europa Island, the influx of warm water appeared to increase the availability of food due to the presence of tropical fish that were unavailable at other times of the year (Le Corre *et al.* 2003). In contrast, Red-billed Tropicbirds at Farallón de San Ignacio in our study initiated breeding when sea surface temperature dropped below 27°C, marking the onset of seasonal upwelling. In the Eastern Pacific, Red-billed Tropicbirds use waters with shallow thermoclines and low salinity near upwelling regions (Spear & Ainley 2005a). Although the patterns indicated above are opposite, in both cases breeding is driven by seasonal oceanographic changes that increased prey availability.

Inter-year difference in mean average laying date and time of laying peak could be a result of an adaptive response by females to synchronize the energy demands of offspring production and provisioning with the period of most favourable environmental conditions (Frederiksen *et al.* 2004, Reed *et al.* 2009). Alternatively, the onset of breeding could have been constrained by the availability of resources during the pre-breeding period rather than the result of an optimal decision by the birds (Drent & Daan 1980). Although at Farallón de San Ignacio breeding was seasonal and coincidental with the time of marine upwelling, in both years it lasted for about 8 months, which allowed for an asynchrony of up to four months between the first and last breeders. So, differences in average laying date

between years appear to reflect that favourable conditions for egg-laying lasted longer. We found that in 2004 the peak of laying occurred in February, coinciding with the peak in chlorophyll concentration and the lowest sea surface temperature, whereas in 2007 the peak of laying occurred in January, two months before the peak in chlorophyll concentration. Most likely, the lower food availability in 2007 reduced the incidence of late egg-laying and thereby advanced the average egg-laying date compared to 2004. Hence, tropicbirds appear to be able to “predict” the marine environmental factors affecting the timing and magnitude of food productivity, which would allow them to time their reproduction to optimize their breeding success and sometimes disfavoured egg-laying late in the season (as in 2007).

Parental attendance and foraging behaviour

The 2007 season in our study was under the influence of a weak El Niño episode (NOAA 2009). There was a sea surface temperature positive anomaly, and less chlorophyll earlier in the season than in 2004. Related to these changes, parental nest attendance, diet and diving depth of adult Red-billed Tropicbirds breeding at Farallón de San Ignacio exhibited inter-annual variability, reflecting less available food in 2007 than in 2004. When El Niño anomalies occur in the Gulf of California, there are changes in phytoplankton communities and fish populations (Kahru *et al.* 2004, Espinosa-Carreón & Valdez-Holguín 2007), and less food available to seabirds (Velarde *et al.* 2004).

At Farallón de San Ignacio, Red-billed Tropicbirds forage only in the upper three meters of the water column and prey mainly on squid and flying fish, as in previous general reports for the family (Le Corre 1997, 2001, Ramos & Pacheco 2003). However, maximum diving depth in 2007 was more than double that in 2004 and differences between both years likely reflected local and regional changes in prey availability as already shown for other species (Croxall *et al.* 1999, Mellink *et al.* 2001, Tremblay & Chérel 2003, Jaquemet *et al.* 2008, Catry *et al.* 2009). A more varied diet, deeper plunge dives and a reduction in the proportion of the main prey items in regurgitates suggests that prey were less available in 2007 and that Red-billed Tropicbirds compensated by increasing their intake of secondary prey items. In some tropical marine birds, plasticity in feeding habits reduces their vulnerability to changes and allows them to breed under varied circumstances (Jaquemet *et al.* 2008, Catry *et al.* 2009). Although limited, our data suggest that Red-billed Tropicbirds can cope with variation in food availability,

in an environment that is variable and displays little predictability at inter-annual scales.

A lower presence of parents at the nest in 2007 suggests that adults devoted more time to foraging in detriment of nest and chick protection. Flexible time-activity budgets have been supported by studies of a wide variety of seabird species, showing that as food supply declines birds spend less time at the colony and more time foraging (Montevicchi 1993, Litzow & Piatt 2003). This flexible time allocation is recognized as an important adaptation for trading off seabird breeding success and breeder survival against the variability in food supply (Litzow & Piatt 2003).

Reproduction and chick growth

Changes in foraging and parental behaviour of red billed Tropicbirds at FSI in 2007 were insufficient to compensate for the low food availability in that year, and consequently parents hatched fewer eggs, chicks fledged with a lower mass and in a worse body condition compared to 2004. Our analyses indicate that parental attendance seems the main driving factor explaining differences in reproductive success between the two years. When feeding conditions change, tropicbirds adjust their parental attendance at the expense of their success: when food is in short supply they spend more time foraging in detriment of parental attendance. This implies less protection and incubation time for eggs, and less protection and possibly food supply for chicks.

The differences in parental attendance and reproductive performance were congruent with differences in oceanographic conditions. There were differences in hatching success (early breeding season), but not in fledging success (late breeding season). So, although high chlorophyll concentration occurs at the end of the season in 2007, the chicks were in worse condition than in 2004, perhaps because the peak of chlorophyll occurred too late (i.e. before it reaches the higher trophic levels) to benefit the tropicbirds.

The response of seabirds to changes associated with El Niño events vary in agreement with the intensity of the event, the geographic area, and the seabird species. In intense events, like that of 1982–83, the response of most central and eastern Pacific seabirds was dramatic: breeding was suspended, nesting areas were deserted and some species experienced adult mortality (Schreiber & Schreiber 1984, Valle *et al.* 1987). During a moderate El Niño event (1986–1987), at Galapagos Islands some species were impacted heavily and abandoned their colonies (Blue-footed Booby and Wedge-rumped Storm Petrel), others abandoned only some

colonies (Nazca Booby), and some other species did not show evident effects (Red-footed Booby and Great Frigatebird, Anderson 1989). At Farallón de San Ignacio, during the moderate El Niño event of 2007, we observed different effects on seabird species breeding. Blue-footed and Brown boobies, and Heermann's Gull had a very low breeding success, and more than 80% of the prior abandoned the colony, at the time that foraging trips were longer and most chicks died of starvation (J. A. Castillo-Guerrero, unpubl. data). Red-billed Tropicbirds, at this location, suffered the least from adverse oceanographic conditions, and they were capable of producing and raising chicks.

Coincidentally to our results, Red-billed Tropicbirds in Daphne and Plaza (in the Galápagos Islands, Snow 1965, Harris 1969) and Ascension (Stonehouse 1962), lack catastrophic responses and successfully breed and raise chicks during El Niño years. We lack the conclusive data to assess why Red-billed Tropicbirds are generally less impacted by El Niño conditions compared to many other seabirds. However, based on the duration of foraging trips and diet, Red-billed Tropicbirds seem to be able to forage much farther from the colony than boobies and gulls. This, and the fact that they forage alone (Spear & Ainley 2005a), might allow them to better exploit small, isolated food patches, and not depend on large concentrations of prey (schooling fishes). In contrast, boobies, Heermann's Gull and Elegant Tern appear to depend on small pelagic schooling fish (see Mellink *et al.* 2001, Velarde *et al.* 2004). Coinciding with the former, seabirds with short foraging intervals close to the coast were more vulnerable to changes in the trophic structure in the Indian Ocean (Cattray *et al.* 2009).

In summary, Red-billed Tropicbirds at Farallón de San Ignacio breed seasonally, coinciding with the winter upwelling period, when they can profit from a higher oceanographic productivity. A number of facts suggest that the higher sea surface temperature of 2007, in comparison to 2004, was related to lower food availability for this species at this colony. In 2007, adults spent more time foraging, dived deeper and obtained different prey species, causing a lower nest attendance and lower hatching success, compared to 2004. The smaller body mass and worse condition of chicks at fledging reflected these conditions. Overall however, despite a potential handicap imposed by El Niño conditions, the species breeds successfully compared with other seabirds in the same colony and exhibits some capacity to cope with the harsher conditions derived from warmer waters during mild El Niño conditions.

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SAMENVATTING

De auteurs onderzochten de broedbiologie van de Keerkringvogel *Phaethon aethereus* op het eiland Farallón de San Ignacio in de Golf van Californië voor de kust van Mexico. De omstandigheden op zee (oppervlaktetemperatuur en concentratie van chlorofyl a) werden in een van twee jaren (2007) beïnvloed door El Niño, in een ander jaar (2004) was dat niet het geval. Van januari tot en met mei werd tweemaal per maand gedurende vijf dagen verbleven op het eiland. De registraties omvatten het tijdstip van begin van broeden, de aanwezigheid van de ouders bij de jongen, en de maximale duikdiepte door de ouders. Daarnaast werd onderzocht wat de jongen aan voedsel kregen, hoe snel ze groeiden en wat hun lichaamsconditie was. Tevens werd het uitkomstpercentage van de eieren vastgesteld, en het percentage van de jongen die vliegvlug werden. In 2007 was de temperatuur van het zeewater hoger dan in het controlejaar, en bovendien was de concentratie van chlorofyl lager. De vogels begonnen eerder met de eileg in 2007. De metingen gaven aan dat er minder voedsel beschikbaar was in 2007: de vogels doken dieper (2,09 m tegen 0,96 m in 2004), de voedselsamenstelling was gevarieerder, en ze bleven langer op zee ten koste van de tijd bij de jongen. Ook was het uitkomstpercentage lager (35% tegen 75% in 2004), en de jongen waren lichter (641 g tegen 739 g) en in slechtere conditie. (DH)

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Appendix 1. Frequency of occurrence of prey species and mean length and weight (\pm SE) in regurgitations of Red-billed Tropicbirds at Farallón de San Ignacio, Mexico, during the 2004 (24 regurgitates) and 2007 (24 regurgitates) breeding seasons. - = not determined.

Prey species	2004	2007	Length (mm)	Weight (g)
Cephalopods				
Dart Squid <i>Loliolopsis diomedea</i>	13	4	93 \pm 8	-
Crustaceans				
Pelagic Red Crab <i>Pleuroncodes planipes</i>	3	1	-	-
Fishes				
Sharpchin Flyingfish <i>Fodiator acutus</i>	11	7	162 \pm 5	49 \pm 10
Flyingfish <i>Hirundichthys</i> sp.	1	1	132	31
Sailfin Flyingfish <i>Parexocoetus brachypterus</i>	1	0	214	-
Ornamented Flyingfish <i>Cypselurus collopterus</i>	0	1	-	-
Mackerel <i>Scomber</i> sp.	2	1	-	-
Longfin Halfbeak <i>Hemiramphus saltator</i>	1	4	181	-
Bigwing Halfbeak <i>Oxyporhampus micropterus</i>	0	2	-	-
Mackerel Scad <i>Decapterus macarellus</i>	0	2	-	-
Shortjaw Leatherjack <i>Oligoplites refulgens</i>	1	1	145	-
Pacific Thread Herring <i>Opisthonema libertate</i>	0	1	-	37
Mojarra <i>Gerres</i> sp.	0	1	132	38