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

José Alfredo Castillo-Guerrero¹,²,*, Miguel A. Guevara-Medina¹ & Eric Mellink¹

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

¹Centro de Investigación Científica y de Educación Superior de Ensenada B. C., Apdo. Postal 360, Ensenada Baja California, México (U.S. mailing address: CICESE P.O. Box 434844, San Diego, California 92143-4844);
*corresponding author (acastillo@ola.icmyl.unam.mx)
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. nebuluxii*, 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, after-
wards, conditions returned to ENSO-neutral (http://
www.cpc.ncep.noaa.gov/products/expert_assessment/
ENSO_DD_archive.shtml). El Niño conditions are char-
acterized 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

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
2007). We marked all eggs with waterproof ink to note
if they were replaced. Chicks were colour-coded indi-
vividually 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 asyn-
chronously early nests was probably small.

Parental attendance, foraging behaviour and diet
We used the proportion of times that parents were pres-
ent 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

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. 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 fledgling 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. Maximum diving depths were 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 ± 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).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>2004 (mean ± SE, sample sizes in brackets)</th>
<th>2007 (mean ± SE, sample sizes in brackets)</th>
<th>Statistical test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laying date (days since 1 October)</td>
<td>113 ± 5.2 (49)</td>
<td>97 ± 5.5 (62)</td>
<td>(\chi^2 = 4.4, P = 0.035)</td>
</tr>
<tr>
<td>Parental attendance during incubation (%)</td>
<td>88 ± 3.1 (36)</td>
<td>68 ± 3.4 (40)</td>
<td>(\chi^2 = 10.3, P = 0.001)</td>
</tr>
<tr>
<td>Parental attendance post-hatching (%)</td>
<td>75 ± 5.2 (24)</td>
<td>58 ± 5.4 (21)</td>
<td>(\chi^2 = 3.1, P = 0.08)</td>
</tr>
<tr>
<td>Maximum diving depth (m) of adults</td>
<td>0.96 ± 0.14 (23)</td>
<td>2.09 ± 0.27 (12)</td>
<td>(\chi^2 = 26, P &lt; 0.001)</td>
</tr>
<tr>
<td>Diet composition (%)</td>
<td>(24)</td>
<td>(24)</td>
<td>(R = 0.084, P = 0.025)</td>
</tr>
<tr>
<td>Flyingfish</td>
<td>40 ± 8.7</td>
<td>37.5 ± 10.1</td>
<td></td>
</tr>
<tr>
<td>Other fishes</td>
<td>13 ± 6.8</td>
<td>43.7 ± 10.1</td>
<td></td>
</tr>
<tr>
<td>Squid</td>
<td>40 ± 8.96</td>
<td>14.6 ± 7.0</td>
<td></td>
</tr>
<tr>
<td>Pelagic red crab</td>
<td>7 ± 4.4</td>
<td>4.2 ± 4.2</td>
<td></td>
</tr>
<tr>
<td>Predicted number of prey species</td>
<td>11 ± 1.4 (24)</td>
<td>24 ± 1.4 (24)</td>
<td>(a = 1.05, b = 0.09, r^2 = 0.98)</td>
</tr>
<tr>
<td>Hatching success (%)</td>
<td>75 ± 7.3 (36)</td>
<td>35 ± 7.6 (40)</td>
<td>(\chi^2 = 11.43, P &lt; 0.001)</td>
</tr>
<tr>
<td>Fledging success (%)</td>
<td>78 ± 6.8 (36)</td>
<td>77 ± 7.2 (36)</td>
<td>(\chi^2 = 0.016, P = 0.89)</td>
</tr>
<tr>
<td>Culmen length at fledging (mm)</td>
<td>51.5 ± 0.37 (25)</td>
<td>50.5 ± 0.57 (23)</td>
<td>(\chi^2 = 2.08, P = 0.15)</td>
</tr>
<tr>
<td>Maximum mass (g) attained by chicks</td>
<td>724 ± 10.5 (25)</td>
<td>600 ± 21.8 (23)</td>
<td>(\chi^2 = 22.3, P &lt; 0.001)</td>
</tr>
<tr>
<td>Chick body condition</td>
<td>0.11 ± 0.028 (25)</td>
<td>-0.12 ± 0.020 (23)</td>
<td>(\chi^2 = 51.5, P &lt; 0.001)</td>
</tr>
</tbody>
</table>

\(\chi^2 = \chi^2\)
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 diomedeae*) 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...
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, Jaquemet 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, Jaquemet 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 breed 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 disfavouring 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 reflect local and regional changes in prey availability as already shown for other species (Croxall et al. 1999, Mellink et al. 2001, Tremblay & Cherel 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 (Montevecchi 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.

Coincidently 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 (Catry 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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REFERENCES


Appendix 1. Frequency of occurrence of prey species and mean length and weight (± 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.

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