

BREEDING BIOLOGY, CHICK GROWTH, AND DIET OF THE LEAST STORM-PETREL *OCEANODROMA MICROSOMA* ON ISLAS SAN BENITO, MEXICO

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ABSTRACT

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The Least Storm-Petrel *Oceanodroma microsoma* is endemic to islands on both coasts of Baja California, in Mexico. It is the smallest seabird species and one of the least studied of the order Procellariiformes. We present a detailed account of its breeding success, chick growth, and diet at Islas San Benito, Baja California, during three consecutive breeding seasons (2013 to 2015) and of sex differences in adult morphology, a study conducted in 2012. Eggs hatched between late July and mid-September, and the fledging period started in mid-October. The timing of breeding varied from year to year: the hatching period began earlier in 2013 than in 2015 and was longer in 2014, while the fledging period started later in 2014 than in 2013. Hatching success (around 80%) and fledging success (about 90%) were consistently high in all three years. Nevertheless, nestlings fledged with longer wings, tails, and bills in 2015. Four species of euphausiids, two species of larval fish, and one species of squid were identified in food samples. Differences in the timing of breeding and chick growth during the period of this study may reflect a variation in food supply associated with anomalous climate conditions recorded in 2014 and 2015.

Key words: Baja California, breeding success, chick growth, diet composition, Least Storm-Petrel, Islas San Benito, timing of breeding

INTRODUCTION

Storm-petrels are among the most abundant seabirds. However, due to their nocturnal arrival at the colonies and their hidden and often inaccessible nests, they remain relatively poorly studied. Most species nest exclusively on islands, where threats such as introduced predators, human disturbance, and contamination have led to the decline of many populations (Croxall *et al.* 2012). Of the 24 storm-petrel species, 38% are listed under a category of protection, and four species are considered Data Deficient by the International Union for Conservation of Nature (IUCN; <http://www.iucnredlist.org>). The breeding biology information for these species is relevant to understand ecological and evolutionary processes, to evaluate the impact of threats at breeding and on sea grounds as well as their vulnerability to changing climate conditions, and to design conservation management guidelines.

The Least Storm-Petrel *Oceanodroma microsoma* is the smallest species of the Hydrobatidae family (weighting approximately 20 g; Brooke 2004) and one of the least studied species of the order Procellariiformes. Its breeding is narrowly distributed among colonies confined to Islas San Benito, off the Pacific coast of the Baja California peninsula, and islands in the Gulf of California, Mexico (Brooke 2004, Howell 2012). Its geographic distribution during non-breeding periods includes coastal and

pelagic waters from southern California to Peru (Veit *et al.* 1996, Spear & Ainley 2007, Howell 2012). Consistent with other Procellariiformes, Least Storm-Petrels lay a single egg, and have a slow reproductive rate, an intense and extended biparental care, and a slow chick development (Brooke 2004). This species commonly breeds in clefts and cavities among and under rocks (Ainley 1984). The diet of Least Storm-Petrels includes planktonic crustaceans and small fish (Ainley 1984). In the last century, introduced mammals negatively affected the main colony sites, but important restoration efforts have recently eliminated this threat (Aguirre-Muñoz *et al.* 2016). The Least Storm-Petrel is listed as Threatened under the Mexican law (Diario Oficial de la Federación 2010), but as Least Concern by the IUCN (BirdLife International 2016).

The breeding biology information for this species is limited to anecdotal observations from brief visits to the colonies or isolated observations. Current knowledge is restricted to partial information on breeding phenology, measurements of eggs, diet, and adult morphometry (Anthony 1896, Murphy 1936, Carmona *et al.* 1994, Pyle 2008, Howell 2012). This article presents an account of the breeding biology of the Least Storm-Petrel, including timing of breeding and breeding success, egg measurements, chick growth, adult morphometry, and diet of individuals nesting on Islas San Benito from 2013 to 2015.

METHODS

Ethics statement

The fieldwork and sample collection were approved by the Secretaría de Medio Ambiente y Recursos Naturales, and Secretaría de Gobernación (Mexico). Extreme care was taken to minimize stress of captured adults and to protect eggs from potential predators. Handling time was kept to a minimum, mostly less than 15 min and always less than 20 min, and the heads of the birds were covered. During this procedure, the birds remained relatively calm and no significant signs of stress were detected. Blood sampling showed no detectable adverse effects; during release, birds flew almost immediately; and sampled individuals recaptured showed good body condition.

Study species and area

This study was carried out from August 2012 to November 2015 at Isla San Benito Oeste (3.64 km²; 28°18'N, 115°35'W, Fig. 1), the westernmost island of the archipelago consisting of three small islands off the Pacific coast of Baja California. These islands have a continental origin and an arid climate, and the dominant vegetation is maritime desert scrub (Junak & Philbrick 2000). The three Islas San Benito support a population estimated at 270 000 breeding Least Storm-Petrels (Wolf *et al.* 2006), which breed in sympatry with Black Storm-Petrels *O. melania* and Leach's Storm-Petrels *O. leucorhoa*, forming a community of approximately two million breeding individuals (Wolf *et al.* 2006). Based on brief visits by early naturalists, it appears that Least Storm-Petrels start laying in June, and records indicate that eggs reach an advanced stage of incubation in late July. The hatching period spans from August to September (Anthony 1896, Murphy 1936) and fledging from September to October (Howell 2012).

These islands are in an oceanographic transition zone where the surrounding waters are divided into two regions (González-Rodríguez *et al.* 2012): 1) the northern marine zone, which is characterized by subarctic waters and upwelling events that persist throughout the year, and 2) a southern regime of upwelling peaks, which occurs during spring and summer, changing from a temperate to a tropical-subtropical domain during summer and autumn (Durazo & Baumgartner 2002, Durazo 2009, 2015).

Nest monitoring and mist netting

We monitored eggs, chicks, and adults from natural nests every four days from 2013 to 2015. We searched for nests among rock crevices using a flashlight in the main nesting area, located on the northern coast of the island in an area called "Cerro Colorado" (Fig. 1). We selected nests in which chicks were more accessible to handling. Nests were individually marked. In 2013, we monitored 39 nests from 9 October to 28 November, when all chicks fledged. During this time, the chick-rearing period was very advanced; therefore, all nests contained hatched chicks. In 2014, we followed 88 nests from 20 August to 26 November. In 2015, we monitored 66 nests from 2 September to 20 November. We did not monitor nests in 2012.

We recorded breeding success using the following metrics: hatching success relative to eggs laid (percentage that hatched), fledging success relative to chicks hatched (percentage that fledged), and overall success (percentage of eggs that resulted in a fledgling).

An egg was considered deserted when the breeding pair did not return to incubate it even though it was in good condition; as broken when we observed signs of damage and abandonment; and as probably predated when the egg went missing. Nest failure also was considered when chicks died at the nest site or when obvious evidence of predation was observed, such as presence of feather remains. In 2014 and 2015, we left the island before the last chick fledged. Therefore, we considered successful nests those with chicks older than 70 d, and that apparently were in healthy condition. This assumption is based on feathering and body condition; after that age, chicks showed fully developed feathers and had already reached peak mass. Similar to Fork-tailed Storm-Petrels *O. furcata*, Least Storm-Petrels show the highest mortality rates in chicks younger than 20 d (Boersma *et al.* 1980, Drummond & Leonard 2009, Y. Bedolla-Guzmán pers. obs.).

During our first visit to the nests, if an egg was present, we measured its length and width (SE 0.1 mm, with calipers) and checked its weight (SE 0.1 g, with a digital balance). As several species of storm-petrels neglect their eggs for around 1 to 6 d (Pefaur 1974, Campos & Granadeiro 1999), we considered an egg deserted when no adult was found after our third visit (i.e., after at least 12 d). If an adult was present during nest controls, we captured it, ringed it with stainless steel rings for individual identification, measured tarsus length (SE 0.1 mm, with calipers), wing length (SD 1 mm, using a wing rule, not flattened), inner tail feather length (\pm 1 mm, using a stopped tail rule), bill length (SE 0.1 mm, with calipers), and checked the weight (SE 0.1 g).

In addition to birds captured during nest monitoring, we also captured adults returning to feed chicks at night using mist nets. Mist nets were deployed from 20h00 to 02h00 during a) 36 nights from September to November 2012; b) 21 nights from September to November 2013; c) 14 nights from August to October 2014; and d) eight nights from September to October 2015. This method was applied to a total of 216 adults, who were captured, ringed with stainless steel rings, and measured as described above. Blood and feather samples were taken from all measured adults for molecular sexing. Molecular sex determination of the 113 adults captured in mist nets in 2012 was carried out following standard methods (Griffiths *et al.* 1996).

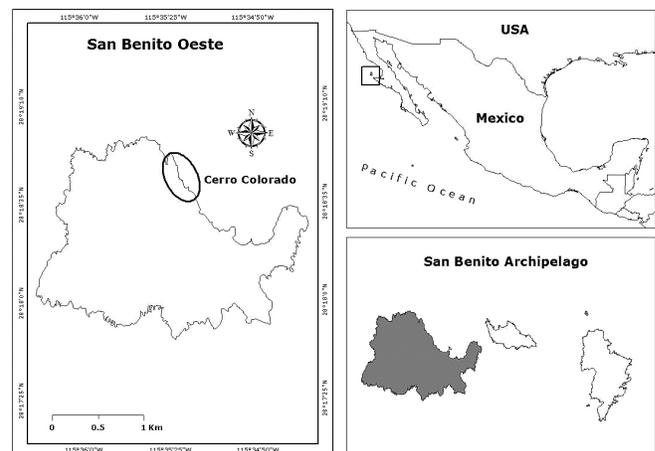


Fig. 1. Location of Isla San Benito Oeste, Baja California Pacific coast, Mexico.

Chick growth

We followed growth patterns by measuring tarsus, wing, bill, and outer as well as inner tail feather lengths every four days. We were able to follow the complete development of the chicks in 2014 and 2015. In 2013, we obtained only partial data on growth; consequently, only some parameters were calculated. The last time pre-fledging measurements were taken was before nestlings left the nest (i.e., 1–4 d before fledging). To estimate the age of chicks of unknown age, in 2014 we followed 11 chicks with known hatch dates from hatching to fledging and obtained a logistic regression from a growth curve for wing length: chick age (d) = $[66.99 \times (\text{wing chord} - 12.21 / 168.59 - \text{wing chord})]^{0.25}$ ($R^2 = 0.94$, $F_{3,198} = 966.90$, $P < 0.001$; Fig. 2). In 2013 and 2015, the ages and approximate hatching dates of chicks already hatched upon our arrival at the island were estimated using the same equation.

Diet composition

We collected regurgitated food samples from adults and chicks opportunistically. Each individual was sampled only once. Adults were sampled while returning to feed the chicks at night, using mist nets (in 2012) or during nest control (2013–2014), and chicks were sampled from natural nests, while being removed from the nests during standard controls. We collected two food samples in 2012, eight samples in 2013, and 19 samples in 2014. We collected regurgitates in 25 mL screw-cap vials during bird handling and fixed them with 70% ethanol. We examined the samples in a laboratory using a stereomicroscope at 40× magnification. Prey taxa were determined with the help of experts and of published keys and guides (Iverson & Pinkas 1971, Wolff 1984, Brinton 1996, Moser 1996, Brinton *et al.* 2000).

Statistical analysis

Statistical analyses were carried out using Statistica 12 (Statsoft Inc. 2014), using $P < 0.05$ to indicate significance; data were plotted using SigmaPlot 11.0 (Systat Software, Inc. 2008). Means are given with standard errors. We tested normality using Kolmogorov-Smirnov tests and homoscedasticity using Levene’s tests. All

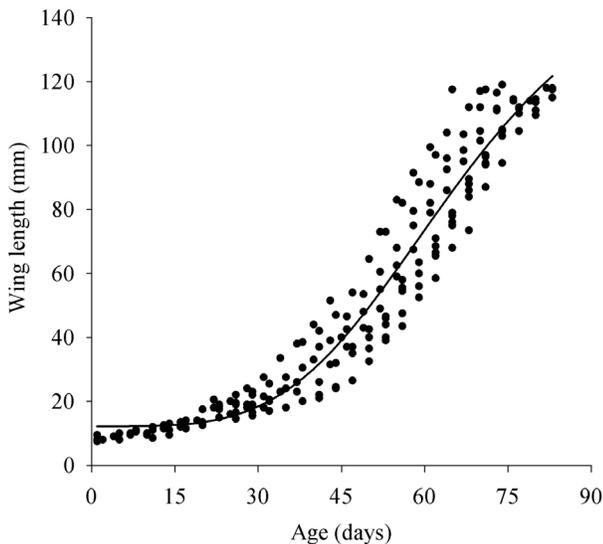


Fig. 2. Wing growth curve of 11 nestling Least Storm-Petrels on Isla San Benito Oeste, Mexico, during the 2014 breeding season.

analyses were carried out on chick means calculated for the field season. Breeding parameters were compared among years using chi-square tests, and hatching dates and fledging dates (Julian calendar) were compared using one-way analysis of variance (ANOVA) or the Kruskal-Wallis test.

RESULTS

Timing of breeding

In 2013, hatching began in late July and, with a few exceptions, continued until early August; in 2014 and 2015, it started around the same time but continued until mid-August (Fig. 3a). The hatching period spanned from 39 to 51 d, and the median hatching date differed between years (Kruskal-Wallis $H_{2,150} = 9.63$, $P = 0.008$); in 2013, chicks hatched 8 d earlier than in 2015 (Table 1). The fledging period started in mid-October and continued through late November in all three years, lasting ~40 d (Table 1, Fig. 3b). The median fledging date also varied among seasons ($H_{2,149} = 12.01$, $P = 0.002$); in 2014, nestlings left the nest 9 d later than in 2013 (Table 1). In 2013, nestlings fledged at a mean age of 81.4 (standard error [SE] 0.4 d; range 77–86 d), whereas in 2014, nestlings left the nest at a mean age of 82.6 (SE 0.7 d; range 72–100 d), and in 2015

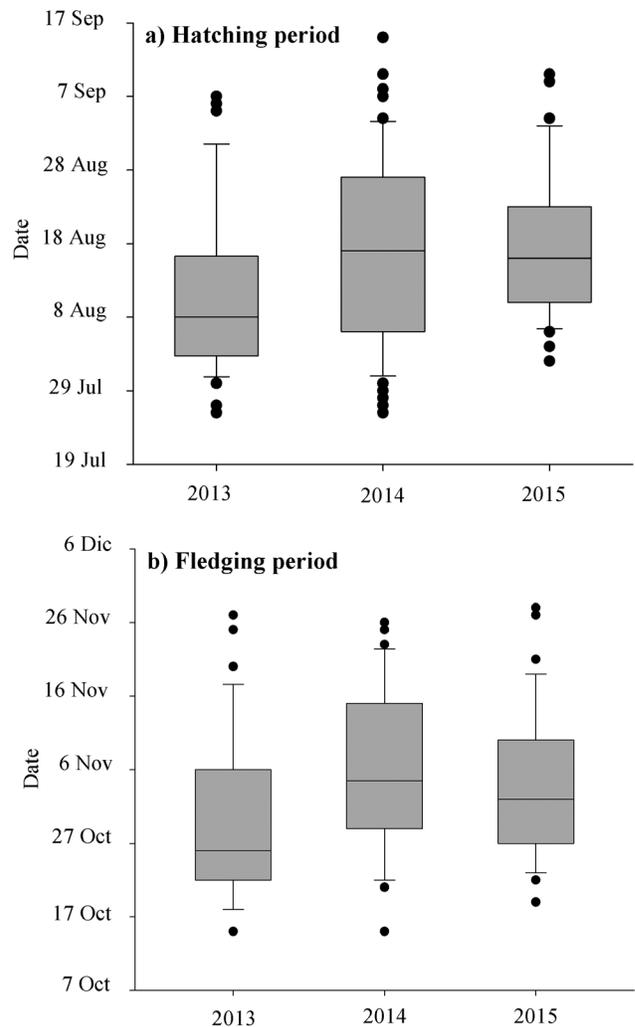


Fig. 3. Hatching and fledging periods of Least Storm-Petrel on Isla San Benito Oeste, Mexico, during the 2013–2015 breeding seasons.

at a mean age of 78.4 (SE 0.6 d; range 70–85 d). Age at fledging differed among years ($H_{2,116} = 23.08$, $P < 0.001$). In 2015, chicks left the nest younger than in the two previous seasons. In 2013, 30% of the chicks that fledged were older than 82 d, whereas in 2014, this percentage increased to 50%, and in 2015, only 17% were older than 82 d.

Breeding success

We calculated hatching success and overall success only in 2014 and 2015, as in 2013, all chicks had already hatched when monitoring started. In 2014 and 2015, hatching success was high (Table 1). The main source of egg failure was desertion (11%), followed by eggs broken (6%), and probable predation (3%;

Table 1). In all three years, fledging success remained consistently high (87%–90%) and did not differ among years ($\chi^2 = 0.01$, $df = 2$, $P = 0.993$; Table 1). The causes of chick mortality were starvation (one in 2013, four in 2014, and four in 2015), death after hatching (one chick in 2014), probable predation (three chicks each year), and flooding (one chick in 2014 was found buried after a tropical storm; Table 1).

Measurements of eggs and adults

In 2014 and 2015, the total of 36 eggs averaged 25.8 mm (SE 0.2 mm; range 24.2–28.7 mm) in length and 18.8 mm (SE 0.1 mm; range 17.2–20.0 mm) in width. The mean egg weight was 4.0 g (SE 0.1 g; range 1.9–5.2 g).

TABLE 1
Variation in breeding timing and breeding success of Least Storm-Petrels on Isla San Benito Oeste, Mexico, during the 2013–2015 breeding seasons

	2013	2014	2015
No. eggs	^a	88	66
No. eggs deserted		9	8
No. eggs broken		4	5
No. eggs probably predated		4	
No. eggs hatched	39	71	53
No. chicks dead after hatching		1	
No. chicks killed by flooding		1	
No. chicks starved	1	4	4
No. chicks probably predated	3	3	3
Hatching success (% of eggs)	^a	81%	80%
Hatching period (days)	43 (26 Jul–7 Sep)	51 (26 Jul–15 Sep)	39 (2 Aug–10 Sep)
Median day of hatching	8 Aug ($n = 38$)	17 Aug ($n = 64$)	16 Aug ($n = 43$)
No. chicks fledged	35	62	46
Fledging success (% of eggs hatched)	90%	87%	87%
Fledging period (days)	43 (15 Oct–27 Nov)	42 (15 Oct–26 Nov)	40 (19 Oct–28 Nov)
Median day of fledging	26 Oct ($n = 35$)	4 Nov ($n = 62$)	2 Nov ($n = 39$)
Overall success (fledglings as a % of eggs)	^a	70%	70%

^a Not calculated, as the breeding season was very advanced at the beginning of the monitoring period and only chicks were found.

TABLE 2
Sex differences of adult Least Storm-Petrels on Isla San Benito Oeste, Mexico, during the 2012 breeding season

Measurement	Females				Males				Test		
	Mean	SE	Min.	Max.	n	Mean	SE	Min.		Max.	n
Body mass (g)	19.4	SE 0.2	16.6	23.5	57	19.5	SE 0.2	20.2	22.7	56	$t = -0.13$, $df = 111$, $P = 0.898$
Wing length (mm)	123.4	SE 0.4	118	129	57	122.0	SE 0.3	117	128	56	$t = 2.8$, $df = 111$, $P = 0.006$
Tarsus length (mm)	21.6	SE 0.08	19.6	23.0	57	21.6	SE 0.08	20.2	22.7	56	$t = 0.147$, $df = 111$, $P = 0.884$
Inner tail length (mm)	55.1	SE 0.4	46.0	61.0	57	53.5	SE 0.3	47.0	59.0	56	Mann–Whitney $U = 1014.5$, $P < 0.001$
Outer tail length (mm)	46.5	SE 0.4	38.0	53.0	57	44.9	SE 0.4	39.0	53.0	53	$t = 2.6$, $df = 111$, $P = 0.010$
Bill length (mm)	11.0	SE 0.06	11.9	10.1	56	11.2	SE 0.06	10.3	12.2	56	$t = -2.2$, $df = 110$, $P = 0.030$

Females had significantly longer wings and tails than males, whereas males had longer bills than females (Table 2). All other morphological parameters did not differ significantly between sexes (Table 2). We found a sex ratio of 1 male: 1 female in the 113 individuals sexed using molecular methods.

Chick growth

We described chick growth during 2014 and 2015, when it was possible to follow the whole developmental period. In 2013, we were able to calculate partial results only. In 2014, the body mass

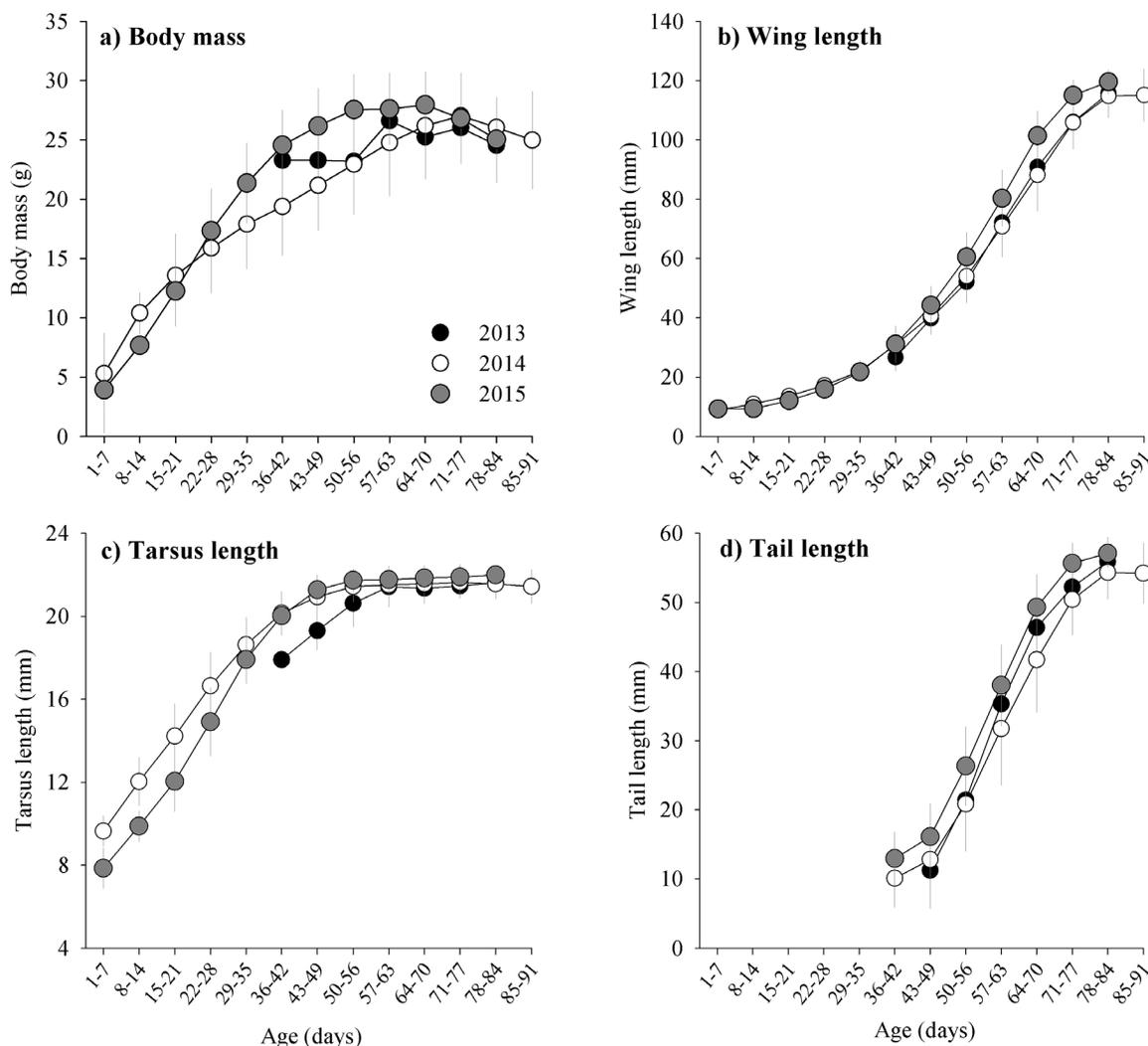


Fig. 4. Chick growth curves of Least Storm-Petrel on Isla San Benito Oeste, Mexico, during the breeding seasons of 2013 ($n = 27$), 2014 ($n = 53$), and 2015 ($n = 36$). The mean and standard error of the mean are given.

TABLE 3
Variation in chick growth parameters of Least Storm-Petrels on Isla San Benito Oeste, Mexico, during the 2013–2015 breeding seasons

Measurement	2013				2014				2015						
	Mean	SE	Min.	Max.	<i>n</i>	Mean	SE	Min.	Max.	<i>n</i>	Mean	SE	Min.	Max.	<i>n</i>
Peak mass (g)	26.0	SE 0.5	16.9	32.3	57	27.4	SE 0.3	23.1	31.8	39					
Pre-fledging mass (g)	22.5	SE 0.4	18.4	27.0	27	24.6	SE 0.3	18.7	29.5	53	23.7	SE 0.4	19.3	29.5	35
Pre-fledging wing length (mm)	115.9	SE 0.7	110	122	27	118.2	SE 0.4	111	126	53	119.0	SE 0.7	108	126	36
Tarsus length asymptote (mm)	21.7	SE 0.1	19.9	22.6	27	21.9	SE 0.08	20.5	23.5	53	22.2	SE 0.09	21.2	23.2	36
Pre-fledging inner tail length (mm)	56.1	SE 0.5	50.0	63.0	26	55.8	SE 0.3	51	63.5	53	56.9	SE 0.4	50.0	60.0	36
Pre-fledging outer tail length (mm)	48.5	SE 0.4	44.0	54.0	27	47.1	SE 0.3	42	52	53	47.9	SE 0.4	42.0	54.0	36
Pre-fledging bill length (mm)	11.0	SE 0.07	10.2	11.7	27	11.3	SE 0.05	10.4	12.2	53	11.5	SE 0.07	10.7	12.4	36

curve (Fig. 4a) showed a long period of rapid growth (from day 9 to 57). This was followed by a short interval of decelerated growth until day 77, and then a quick mass loss until fledging. In contrast, in 2015 the rapid weight increase was shorter from day 8 to day 43, and peak mass occurred from day 44 to day 74 (Fig. 4a). Peak mass differed among years (Mann–Whitney $U_{102} = 841$, $P = 0.04$) and was higher in 2015 (Table 3). Body mass was described by quadratic regressions (Table 4), while the growth of wings (Fig 4b), tarsi (Fig. 4c), and inner tail lengths (Fig. 4d) were well described by logistic regressions (Table 4).

Pre-fledglings from 2015 developed longer wings ($F_{2,121} = 9.12$, $P < 0.001$), tarsi (Kruskal-Wallis test, $H_{2,121} = 12.33$, $P = 0.002$,

and bills ($F_{2,121} = 11.40$, $P < 0.001$) than nestlings from the previous two seasons (Table 3). Nestlings from 2015 left the nest with an inner tail longer than nestlings from 2014 ($H_{2,121} = 7.72$, $P = 0.021$; Table 2). In 2014, pre-fledglings had higher body mass than in 2013 ($F_{2,121} = 7.17$, $P < 0.001$; Table 3).

Diet composition

We found a range of prey items in regurgitated food samples, including crustaceans, squid, and larval fish. Only two species of larval fish were found in 2012: *Vinciguerria lucetia* and *Synodus lucioceps*. In 2013, we identified three species of euphausiids (*Euphausia gibboides*, *Nyctiphanes simplex*, and *Thysanoessa*

TABLE 4
Chick growth curves of Least Storm-Petrels on Isla San Benito Oeste, Mexico, during the 2014 and 2015 breeding seasons

Parameter	Curve shape	Equation
Body mass	Quadratic	2014: mass (g) = $4.45 + 0.51 \times \text{age} - 0.003 \times \text{age}^2$, $R^2 = 0.64$, $F_{3,3037} = 2\,714.0$, $P < 0.001$ 2015: mass (g) = $-2.81 + 1.02 \times \text{age} - 0.008 \times \text{age}^2$, $R^2 = 0.70$, $F_{3,1846} = 2\,138.7$, $P < 0.001$
Wing length	Logistic	2014: wing (mm) = $12.99 + 155.82/1 + (\text{age}/68.14)^{-3.9}$, $R^2 = 0.96$, $F_{3,963} = 7\,121.12$, $P < 0.001$ 2015: wing (mm) = $12.83 + 149.30/1 + (\text{age}/62.3)^{-4.4}$, $R^2 = 0.98$, $F_{3,691} = 1\,0318.4$, $P < 0.001$
Tarsus length	Logistic	2014: tarsus (mm) = $9.88 + 12.21/1 + (\text{age}/22.69)^{-2.9}$, $R^2 = 0.88$, $F_{3,969} = 2\,417.24$, $P < 0.001$ 2015: tarsus (mm) = $9.46 + 12.76/1 + (\text{age}/2\,698)^{-4.3}$, $R^2 = 0.94$, $F_{3,696} = 3\,472.8$, $P < 0.001$
Inner tail length	Logistic	2014: inner tail (mm) = $8.07 + 51.34/(1 + (\text{age}/61.37)^{-8.0})$, $R^2 = 0.88$, $F_{3,677} = 1\,576.9$, $P < 0.001$ 2015: inner tail (mm) = $9.54 + 52.11/(1 + (\text{age}/58.40)^{-8.0})$, $R^2 = 0.93$, $F_{3,437} = 2\,004.5$, $P < 0.001$

TABLE 5
Diet composition of Least Storm-Petrels on Isla San Benito Oeste, Mexico, during the 2012–2014 breeding seasons

	2012 <i>n</i> = 2			2013 <i>n</i> = 8			2014 <i>n</i> = 19		
	<i>F</i> ^a		<i>V</i> ^b	<i>F</i>		<i>V</i>	<i>F</i>		<i>V</i>
	<i>n</i>	%	%	<i>n</i>	%	%	<i>n</i>	%	%
Euphausiacea				5	63	25	8	42	19
<i>Euphausia gibboides</i>				1	13				
<i>Nematoscelis difficilis</i>							3	16	
<i>Nyctiphanes simplex</i>				2	25		3	16	
<i>Thysanoessa spinifera</i>				2	25				
Unidentified							2	11	
Amphipoda							1	5	1
Unidentified							1	5	1
Cephalopoda				1	13	18			
<i>Doryteuthis opalescens</i>				1	13				
Unidentified									
Fish larvae	2	100	100	6	75	57	11	58	67
<i>Vinciguerria lucetia</i>	2	100		2	25		2	11	
<i>Synodus lucioceps</i>	1	50							
Unidentified	1	50		4	50		9	47	

^a *F* (frequency of occurrence) is the percentage of samples in which prey items of each type were found, and

^b *V* is the estimated volume in percentage for each main prey group.

spinifera), one species of squid *Doryteuthis opalescens*, and one species of larval fish (*V. lucetia*). In 2014, although most of the samples were too digested for prey identification, we were able to identify the euphausiids *Nematoscelis difficilis* and *N. simplex* as well as larval fish *V. lucetia*. In 2013 and 2014, Least Storm-Petrels consumed a larger volume of larval fish than euphausiids (Table 5).

DISCUSSION

This study provides the first detailed account of breeding phenology, breeding performance, chick growth, and diet during the breeding of Least Storm-Petrels. We determined that the hatching period started in late July, and fledging extended until late November. These results contrast with previous observations that indicated that the hatching period spanned from mid-August to early-September at Isla San Benito Oeste (Anthony 1896, Murphy 1936) and the fledging period from September to October (Howell 2012). This discrepancy might result from the fact that our study was more detailed, facilitated by a longer stay on the island compared to the studies conducted previously, which lasted a shorter period of time.

The timing of breeding differed among years: the hatching period started earlier in 2013 than in 2015 and was longer in 2014, while the fledging period started later in 2014 than in 2013. Differences in the timing of breeding in other storm-petrel species have been related to food supply (Boersma *et al.* 1980) and weather conditions (Drummond & Leonard 2009). On Isla San Benito Oeste, differences in breeding phenology among years might be in response to two anomalous climatic conditions observed in the region during the time span of this study. The first difference is related to the anomalously warm sea-surface temperature that prevailed along the Baja California Pacific coast from the winter of 2013–2014 until April 2015. This phenomenon, identified as the Pacific Warm Anomaly—also known as the “blob”—affected the northeast Pacific, causing low productivity and subsequent decrease in prey availability (Bond *et al.* 2015, Kintisch 2015). The second difference was related to a strong El Niño, which lasted from September to December 2015 (Robinson 2016). The differences in the duration of the hatching period observed in 2014 could be related to lower food availability, consequence of the anomalous conditions. Some birds could have been forced to forage for longer periods in search of less abundant prey, extending the time needed for incubation and, consequently, prolonging the hatching period.

During our study, the anomalous oceanic conditions severely affected other seabird species in the region. For instance, on some Baja California Pacific islands, breeding individuals of Brown Pelican *Pelecanus occidentalis* and Brandt’s Cormorant *Phalacrocorax penicillatus* massively deserted their nests in 2015 (Bedolla-Guzmán *et al.* 2016). Similarly, marine mammals, such as California sea lions *Zalophus californianus* and Guadalupe fur seals *Arctocephalus philippii townsendi* breeding on Islas San Benito, decreased in abundance, with pup production reduced to 52%–55% in 2015 compared with 2014 (California sea lion pup production: 2014 = 8792 pups, 2015 = 4585; Guadalupe fur seal pup production: 2014 = 71 pups, 2015 = 39) (Elorriaga-Verplancken *et al.* 2016).

Studies in the Gulf of California indicate that the Least Storm-Petrel breeding seasons are asynchronous among colonies, starting earlier than on Islas San Benito. In the northern Gulf islands (e.g., Isla Partida Norte, 28°53'N, 113°02'W), laying extends from May

to June and the fledging period from August to September (Howell 2012, Grupo de Ecología y Conservación de Islas, A.C., unpubl. data). On the other hand, in the southern Gulf colonies (La Lobera, Isla Espíritu Santo, 24°35'N, 110°24'W), laying starts around mid-March and fledging around the beginning of June (Carmona *et al.* 1994). The differences could be related to the marked seasonal-productivity peak, which occurs during winter and spring in that region (Álvarez-Borrego 2010). However, this information should be considered cautiously, as there are no detailed studies for any area in the Gulf of California.

Breeding parameters did not differ among the years studied, as the overall success was consistently high (up to 70%; Table 1). Similarly, Black Storm-Petrels that breed on Islas San Benito also had high hatching and fledging success rates during our study (72%–87%) (Y. Bedolla-Guzmán, unpubl. data). A comparison with storm-petrels investigated elsewhere may offer clues as to why Islas San Benito had such a high success rate. Other members of the genus *Oceanodroma* have also exhibited high breeding success (*O. furcatus* — Boersma *et al.* 1980; *O. homochroa* — Ainley 1995; *O. leucorhoa* — Huntington *et al.* 1996). In contrast, the success rate of species breeding on islands with invasive predators such as the house mouse *Mus musculus* was only 54% (*Pelagodroma marina* — Campos & Granadeiro 1999). Buffer mechanisms that may keep breeding success high and constant in procellariiform species include changes in diet composition (García-Godos *et al.* 2002, Hedd *et al.* 2009, Quillfeldt *et al.* 2010), a flexible foraging strategy (Baduini & Hyrenbach 2003), and regulation of chick provisioning parameters (Weimerskirch *et al.* 2001, Büsser *et al.* 2004, Quillfeldt *et al.* 2007).

Breeding success of other burrow-nesting seabirds, such as alcids breeding on islands off the Pacific Baja California coast, may provide evidence of the impacts of anomalous ocean conditions, such as the “blob” or El Niño, on species with similar foraging strategies as storm-petrels. The Guadalupe Murrelet *Synthliboramphus hypoleucus*, on Isla Guadalupe, had a breeding success rate of 80.9% in 2014 and 2015 (Hernández-Montoya *et al.* 2015, 2016); similarly, the Scripps’s Murrelet *S. scrippsi*, on Islas Todos Santos, had an overall success rate of 90% in 2015 (Bedolla-Guzmán *et al.* 2016). In contrast, the Scripps’s Murrelet had a very low success rate (28%) on Islas San Benito in 2014 (Ramos-Rendón *et al.* 2014), and the Cassin’s Auklet *Ptychoramphus aleuticus* breeding on Isla San Roque and Isla Asunción had a low breeding success rate in 2015 (40%, Bedolla-Guzmán *et al.* 2016).

In 2015, chick growth was higher than during the two previous seasons, and this was reflected in nestlings of higher quality, as chicks showed longer wings, tarsi, and bills. This variable growth pattern observed among the years is in accordance with other species such as Black Storm-Petrel breeding on Isla San Benito (Y. Bedolla-Guzmán, unpubl. data) and Fork-tailed Storm-Petrel in Alaska (Boersma *et al.* 1980, Boersma & Parrish 1998). In contrast to Least Storm-Petrel, Leach’s Storm-Petrel on the east coast of North America appears to exhibit uniform growth rates among years (Ricklefs *et al.* 1985). It has been suggested that high chick growth is reached when provisioning rates and food quality are high (Boersma & Parrish 1998). On Isla San Benito, food availability was probably more favorable in 2015. Similar to Least Storm-Petrels, other procellariiform species such as Thin-billed Prions *Pachyptila belcheri* (Quillfeldt *et al.* 2007), Yellow-nosed Albatross *Thalassarche chlororhynchos* (Weimerskirch *et al.* 2001),

and Fairy Prions *P. turtur* (Manno *et al.* 2014) can maintain a high fledging success rate despite unfavorable conditions. However, in those species the quality of the offspring was negatively correlated with fledging success.

Least Storm-Petrels preyed mainly on larval fish during all three years. One of the prey, *V. lucetia*, is a tropical-subtropical midwater fish that occurs from Chile to central California and is more abundant during warm events compared with cold events (Funes-Rodríguez *et al.* 2010, Jiménez-Rosenberg *et al.* 2010). In fact, in 2015, according to records, *V. lucetia* larvae were very abundant off the coast of Baja California, perhaps the result of the combination of the “blob” with El Niño 2015–2016 (McClatchie *et al.* 2016). This could explain why in 2014 adults fed their chicks mainly with larval fish, but further study is necessary to evaluate diet composition in cold years. Three euphausiids identified in food samples, *E. gibboides*, *N. simplex*, and *N. difficilis*, are abundant off the coast of Baja California, with *N. simplex* being more abundant in coastal waters and *N. difficilis* more abundant in oceanic waters (Lavaniegas & Ambriz-Arreola 2011).

In conclusion, we suggest that differences in the timing of breeding and chick growth among years may reflect a variation in food supply associated with the anomalous climate conditions recorded in 2014 and 2015. Long-term data would be necessary to better evaluate the effect of local oceanographic conditions on diet and breeding biology of Least-Storm Petrels in the Baja California region.

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