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Seasonal ecology of a migratory nectar-feeding bat at the edge of its range

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Migratory species that cross geopolitical boundaries pose challenges for conservation planning because threats may vary across a species' range and multi-country collaboration is required to implement conservation action plans. The lesser long-nosed bat (*Leptonycteris yerbabuenae*) is a migratory pollinator bat that was removed from the Endangered Species List in the United States in 2018 and from threatened status in Mexico in 2013. The seasonal ecology and conservation status of the species is well understood in the core part of its range on mainland Mexico and in the southwestern United States, but relatively little is known about the species on the Baja California peninsula in northwestern Mexico, a part of its range range separated by the Gulf of California. We studied the seasonal ecology of lesser long-nosed bats on the Baja peninsula at 8 focal roosts along a 450-km north-to-south transect to test hypotheses about migratory or residential status of the species on the Baja peninsula. We provide evidence of an extensive population of lesser long-nosed bats on the Baja peninsula that is primarily seasonally migratory and includes 2 mating roosts with males on the southern part of the peninsula. Seasonal ecology of lesser long-nosed bats was closely associated with the flowering and fruiting season of the cardón (*Pachycereus pringlei*), the dominant columnar cactus on the peninsula. However, we discovered that some female lesser long-nosed bats arrive and give birth at southern roosts in mid-February, about 2 months earlier than other migratory populations in more northern Sonoran Desert habitats. We documented the loss of nearly a third of the known maternity roosts during the study, demonstrating that action to protect key roosts remains a high priority. Migratory pollinators are particularly vulnerable to climate and land-use changes and we recommend continued monitoring and research to guide effective range-wide conservation of the species.

Las especies migratorias o con rangos de distribución amplios que incluyen fronteras geopolíticas, representan desafíos particulares para la planificación de estrategias de conservación, ya que las amenazas así como las tendencias poblacionales pueden variar a lo largo de su rango geográfico y se requiere la colaboración de múltiples países para implementar planes de acción que permitan su conservación. El murciélago magueyero menor (*Leptonycteris yerbabuenae*) es un murciélago polinizador migratorio que recientemente fue sacado de la lista de especies en peligro en los Estados Unidos en 2018 y en México en 2013. La ecología estacional y el estatus de conservación de esta especie, ha sido bien estudiado en el centro de su rango de distribución en México continental, pero se sabe muy poco acerca de la especie en la Península de Baja California en el noreste de México, región que está separada del resto del rango por el golfo de California. Nosotros estudiamos la ecología estacional del murciélago magueyero menor, en ocho cuevas a lo largo de un transecto de 450 km norte-sur, en la Península de Baja California y pusimos a prueba la hipótesis del status migratorio o residente de sus poblaciones en esta región. Proporcionamos la primera evidencia de una extensa población de esta especie en la península, a cual es principalmente migratoria estacional e incluye dos cuevas de reproducción ubicadas al sur de esta región. La ecología estacional del murciélago magueyero menor estuvo fuertemente asociada con la estación de floración y fructificación del cardón (*Pachycereus pringlei*), el cactus columnar dominante en la península. Nosotros también descubrimos que algunas hembras llegan y dan a luz en las cuevas más sureñas, a mediados de febrero, cerca de dos meses antes que otras poblaciones migratorias, en el desierto de Sonora del norte. Durante el tiempo de este estudio, documentamos la destrucción de una de las cuevas de maternidad, lo que demuestra la necesidad de acciones de conservación para proteger estos refugios. Los polinizadores migratorios son particularmente vulnerables a cambios en el uso del suelo y al cambio climático y recomendamos continuar con el monitoreo y la investigación, con el fin de guiar su conservación a lo largo de todo el rango de distribución de la especie.

Key words: Baja California Sur, cactus, conservation, *Leptonycteris yerbabuenae*, Mexico, migration, pollinator, range edge

Migratory or wide-ranging species that cross geopolitical boundaries pose particular challenges for conservation planning as threats and population trends may vary across a species' range, and multi-country collaboration is required for implementing conservation action plans (Medellín et al. 2004). Conservation attention often focuses on core populations where data may be more easily obtainable, but threats to and resiliency of populations may differ across a species' range (Channell and Lomolino 2000). Understanding ecological differences across a species' range is important for predicting range shifts and the impacts of climate change on patterns of global biodiversity, particularly for areas where land use and climate change are predicted to significantly alter habitat suitability (Zamora-Gutierrez et al. 2018). Studying ecological dynamics at range edges answers basic questions about biogeographic limits, but is also needed to assess global extinction risk and inform conservation priorities at a species level (Channell and Lomolino 2000).

The lesser long-nosed bat (*Leptonycteris yerbabuenae*) is a migratory nectar- and fruit-feeding bat that forms large aggregations (up to hundreds of thousands of bats) in caves and mines and migrates from central Mexico to the southwestern United States during the spring and summer bloom of agave and columnar cacti (Wilkinson and Fleming 1996; Ceballos et al. 1997; Horner et al. 1998; Rojas-Martínez et al. 1999; Stoner et al. 2003). The species was federally protected as endangered in the United States at the northern extent of its seasonal migratory range in the late 1980s (Cole and Wilson 2006), and recently became the first bat to be removed from the Endangered Species List in the United States (USFWS 2018). The species was also listed in Mexico as threatened in 1994, and delisted in 2013 (Medellín et al. 2018). Population dynamics, migratory patterns, and reproductive phenology are relatively well-known in mainland Mexico (Wilkinson and Fleming 1996; Ceballos et al. 1997; Horner et al. 1998; Rojas-Martínez et al. 1999; Stoner et al. 2003) and monitoring of key roosts in this central part of the range supported the delisting of the species in Mexico (Medellín et al. 2018).

In contrast, the population status, seasonal ecology, and migratory habits of lesser long-nosed bats on the Baja California peninsula, a part of the species' range separated by the Gulf of California (Fig. 1), have received little attention. Habitats on the Baja California peninsula are identified as at high risk for loss of environmental suitability for bats over the next 30 years due to land use and climate change (Zamora-Gutierrez et al. 2018). In the USFWS species recovery plan, only 2 roost sites for lesser long-nosed bats were listed on the Baja California peninsula (USFWS 1995) and the assumption

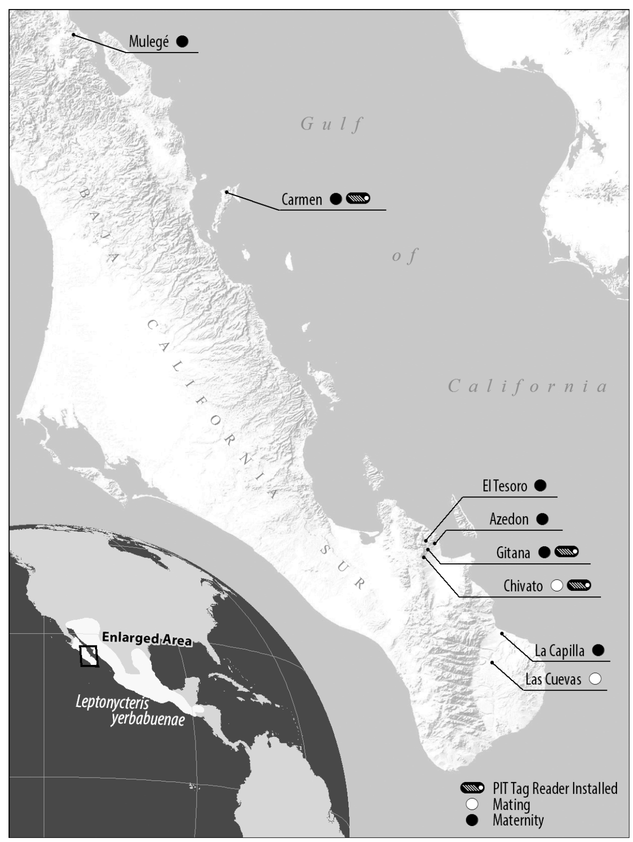

Fig. 1.—Map of locations of 8 lesser long-nosed bat (*Leptonycteris yerbabuenae*) roosts studied on the Baja California peninsula in northwestern Mexico. The Mulegé and Carmen roosts occur in the mid-peninsular region and the other roosts are located in the southern Cape region of the Baja peninsula.

was made that the Baja population was limited to year-round residents that overwinter in the southern part of the peninsula (Fleming et al. 1993; Rojas-Martínez et al. 1999). Earlier work has shown that lesser long-nosed bats are widespread during April and May on the Baja peninsula and associated islands in the Gulf of California (Frick et al. 2007, 2009) and are regular visitors to flowers of the cardón cactus (*Pachycereus pringlei*, Cactaceae—Frick et al. 2013). Assessing the seasonal phenology and population status of lesser long-nosed bats on the Baja peninsula provides an opportunity to study how seasonal ecology may differ at the northwestern edge of the range and fills existing data gaps for assessing range-wide threats and population status to determine species-level conservation needs of this binational migratory species.

The migratory or resident status of lesser long-nosed bats on the Baja peninsula has long been speculated about in the literature (Woloszyn and Woloszyn 1982; Fleming et al. 1993; Rojas-Martínez et al. 1999). Two alternative hypotheses of migratory behavior on the Baja peninsula have been proposed: 1) Female bats seasonally migrate over the Gulf of California (potentially using islands as "stepping stones"—Ramirez 2011), returning to maternity roosts on the Baja peninsula to give birth and raise young when columnar cacti and agave are in bloom in April and May. This pattern would be consistent with the seasonal phenology of populations that migrate to the Sonoran Desert in northern mainland Mexico and the southwestern United States where females arrive and give birth synchronously with the bloom of columnar cacti and agaves (Rojas-Martínez et al. 1999). 2) Females reside year-round on the Baja peninsula and spend the winter months in the southern Cape region of Baja (south of La Paz) where they depend on winter-blooming agaves (Fleming et al. 1993). If the latter hypothesis were true, we would expect to find year-round occupancy and increased colony sizes at southern roosts during winter months when bats are absent from maternity sites in mid-peninsular areas.

We measured seasonal roost occupancy, reproductive timing, and changes in body mass of lesser long-nosed bats on the Baja peninsula to assess the seasonal ecology of the species on the edge of its range. We compared seasonal occupancy patterns and reproductive timing at roosts in the southern Cape region of Baja to roosts in the mid-peninsular region to distinguish between the 2 competing hypotheses of seasonal presence on the Baja peninsula. We hypothesized that body mass of bats on the Baja peninsula would vary seasonally and be highest during spring and summer months when nectar and fruit from columnar cacti, the dominant food resource, are abundantly available. We also assess the conservation status of known roosts in Baja and discuss the conservation implications of our findings.

Materials and Methods

Study area.—We studied the seasonal ecology of lesser long-nosed bats in Sonoran Desert habitats of the Baja California peninsula in northwestern Mexico (Fig. 1). The Baja California peninsula has distinct ecoregions (http://bajaflora.org/) with characteristic dominant plant communities (Rebman and Roberts 2012). Bat roosts occurring in the mid-peninsular region occurred in the Gulf coast ecoregion in habitats dominated by spring- and summer-blooming columnar cacti, such as cardón (*P. pringlei*) and organ pipe (*Stenocereus thurberi*, Cactaceae). Bat roosts identified in the southern peninsula region occurred in the sarcocaulescent shrubland ecoregion bordering tropical dry forest (http://bajaflora.org/). Habitats near southern roosts had high densities of columnar cacti dominated by the same spring- and summer-blooming species (*P. pringlei* and *S. thurberi*) but also contained the cardón-barbón columnar cactus (*P. pecten-aboriginum*, Cactaceae) that blooms November–February. Agave species occurred in all ecoregions where bat roosts were located but at lower densities and with less predictable flowering phenologies (Rebman and Roberts 2012; Webb and Starr 2015).

Roost locations and seasonal use.—We identified existing and new roost localities of lesser long-nosed bats on the Baja peninsula by searching the literature, querying museum capture records, and talking to local communities and other researchers. We visited 8 focal roosts in at least 3 of 4 seasons from October 2013 through April 2016 (Figs. 1 and 2). Seasons were defined as 3-month periods relating to general phenology of nectar and fruit availability in the region: November–January (low), February–April (nectar), May–July (nectar and fruit), and August–October (fruit). We visually estimated the number of lesser long-nosed bats present and identified presence of other species during surveys inside the focal roosts (Table 1). Visual counts of lesser long-nosed bats are extremely challenging because the bats are active and fly readily when disturbed. We initially took photographs of clusters of bats to estimate density of individuals in a cluster and then approximated colony size by extrapolating surface area by cluster density. We show these approximated colony sizes in Fig. 2, but because colony size estimates were imprecise, we used presence–absence of bats at roosts in statistical analyses on seasonal patterns of roost occupancy.

Passive integrated transponder tag monitoring.—We initiated a long-term monitoring program using passive integrated transponders (PIT tags) and installing Biomark IS1001 radiofrequency identification transceivers attached to 15 m flexible cord antennae (Biomark, Inc., Boise, Idaho) at 3 roost locations:

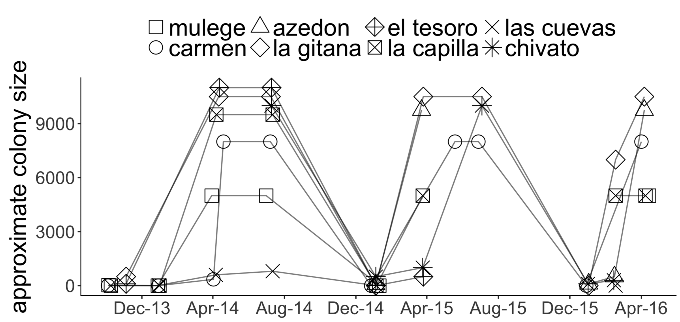

Fig. 2.—Seasonal patterns of roost occupancy at 8 roosts of lesser long-nosed bats (*Leptonycteris yerbabuenae*) in Baja California Sur, Mexico. Lines connect survey occasions sampled in consecutive seasons. The Mulegé and Carmen roosts occur in the mid-peninsular region and all other sites occur in the southern peninsula.

Table 1.—Description and protection status of 13 roosts of lesser long-nosed bats (*Leptonycteris yerbabuenae*) in Baja California Sur, Mexico. Bold indicates roosts not previously reported; gray shading highlights roosts recently destroyed.

Site	Feature	Roost type	Protection status	Other bats present	Region
Mina La Julia[a]	Mine	Seasonal stopover	Unknown	*Choeronycteris mexicana* *Myotis californicus*	Northern Baja
San Sebastián	Cave	Seasonal stopover	Unprotected, known by local ranchers	*Macrotus californicus*	Mid-Baja
Mulege	Modified cave	Maternity	Unprotected, near town sprawl	*Macrotus californicus*	Mid-Baja
Coronados	Sea cave	Maternity	Protected in National Park	*Myotis vivesi*	Gulf Island Mid-Baja
Carmen	Cave	Maternity	Protected on privately owned island	*Macrotus californicus*	Gulf Island Mid-Baja
Mina San Jose	Mine	Maternity	Destroyed after 2006	*Macrotus californicus*	Gulf Island Mid-Baja
Cueva de la Iglesia	Cave	Maternity	Vandalized with fire and abandoned in 2018	*Macrotus californicus* *Myotis* spp.	Southern Baja
Chivato	Mine	Mating and Maternity	Protected on private ranch	*Macrotus californicus* *Natalus mexicana*	Southern Baja
La Gitana	Mine	Maternity	Protected on private ranch	*Macrotus californicus*	Southern Baja
Azedon	Mine	Maternity	Protected on private ranch	*Macrotus californicus*	Southern Baja
El Tesoro	Mine	Maternity	Collapsed in 2015	*Macrotus californicus* *Natalus mexicana*	Southern Baja
La Capilla	Mine	Maternity	Destroyed in 2017	*Macrotus californicus* *Natalus mexicana* *Mormoops megalophylla*	Southern Baja
Las Cuevas	Cave	Mating and Maternity	Unprotected, known by locals. Pictures and location occasionally posted online	*Macrotus californicus* *Tadarida brasiliensis* *Myotis velifer peninsularis*	Southern Baja

[a] Source: Guevara-Carrizales et al. (2010).

2 mines (Chivato and La Gitana) in the southern peninsula and a natural cave (Isla Carmen Cave) in the mid-peninsular region (Fig. 1). IS1001 readers were installed and continuous monitoring commenced at the Chivato Mine in January 2015 and at the La Gitana Mine in January 2017. We first marked bats with PIT tags (see below) at the Carmen Cave in spring 2013, but due to some early technical problems with an initial system, we were unable to reliably collect data at this site until the system was replaced in March 2015. We tagged 1,107 lesser long-nosed bats from 6 different roost locations from 2013 to 2017, with the majority of tagging occurring at the focal roosts Carmen and Chivato (Table 2).

Bat capture and handling.—We captured bats by either placing harp traps at roost entrances or entering a site and using hoop nets. We determined sex, age, and reproductive condition and measured mass and forearm length of captured individuals (Racey 2009). We marked bats with pit tags by subdermally inserting a 12-mm tag premounted into a sterilized needle loaded in an applicator gun (Biomark, Inc.) under the dorsal skin (Kunz and Weise 2009). The insertion site was sealed using a fast-acting medical adhesive (3M Vetbond Tissue Adhesive).

To determine reproductive timing at maternity sites, we assessed reproductive condition of adult females and development stage of young in early April. Young were classified into 4 categories based on pelage and size characteristics corresponding to developmental stage (newborn, infant, juvenile, and volant; see Supplementary Data SD1). Since females typically leave young inside the roost while foraging at night, we assessed development stage class of young by waiting for adult females to leave and visually surveying young inside the roost.

Table 2.—Total number of lesser long-nosed bats (*Leptonycteris yerbabuenae*) marked with passive integrated transponder (PIT) tags from 2013 to 2017 from 6 roost locations in Baja California Sur, Mexico. Gray shading indicates years and sites with continuous active monitoring with Biomark IS1001 transceivers.

Site	Number of bats tagged					Total
	2013	2014	2015	2016	2017	
Carmen	222	36	102	60	100	520
Chivato			207	57	57	321
La Gitana				47	96	143
Azedon				25		25
La Capilla		53				53
Las Cuevas	17	28				45

To minimize disturbance, we used red lights and visually classified as many young as possible in 15 min.

Research activities followed ASM guidelines (Sikes et al. 2016) and were approved by the UC Santa Cruz Institute of Animal Care and Use Committee (IACUC) under protocol Frickw1602. All necessary permits were issued by Dirección General de Vida Silvestre, SEMARNAT, to RAM with collaborative permissions to WFF.

Seasonal occupancy analysis.—To determine whether seasonal occupancy patterns differed in mid-peninsular and southern regions, we used generalized linear models with binomial errors and the bias-reduction method (package brglm in R v. 3.1.2) and fit 5 a priori candidate models with observed presence or absence of bats at a roost as the binary response and region (mid-peninsula and southern peninsula) and season as categorical predictors (Table 3). We used Akaike's information criteria (AIC) for model selection (Burnham and Anderson 2002). We also calculated the fraction of tagged bats from each tagging occasion detected by roost antennae each day from January 2015 to February 2018 at 2 focal roost sites in the mid- and southern peninsula (Carmen and Chivato, respectively; Fig. 3).

Reproductive timing and body mass of females.—We used generalized linear models with binomial errors to test if the probability that reproductive stage of adult females or young-of-year development stage differed between regions for sites sampled in early April to determine whether timing of reproduction varied between the mid-peninsular and southern regions. In all logistic regression analyses, we used a bias-reduction method (package brglm in R v. 3.1.2) to deal with complete separation present in the data. We used a general linear regression with body mass as response and a categorical predictor of reproductive status with 5 categories (nonreproductive, pregnant, lactating, lactating and carrying pup, and post-lactating) to describe body mass changes in females associated with reproduction. We were unable to test for seasonal effects on body mass of females because changes in body mass of females related to reproduction were confounded with seasons.

Table 3.—Model comparison for seasonal roost occupancy logistic regression. Models were fit with a binomial distribution and a logit link using a bias-reduction method implemented in the brglm function from package brglm in program R. ΔAIC = difference in Akaike's information criterion value between the focal model and the top-ranked model in the set. AIC weight = the relative likelihood of the focal model.

Model structure	ΔAIC	AIC weights
Logit(Pr(Occupancy)) ~		
Season	0	0.65
Season + region	1.35	0.33
Season * region	8.59	0.01
1 (null)	9.92	0.00
Region	11.57	0.00

Seasonal variation in body mass and reproductive status of males.—We captured male lesser long-nosed bats in all seasons in the southern peninsula and used general linear regression with body mass as the response variable and season as a categorical explanatory variable to test whether body mass of males varied seasonally. We predicted that bats would have higher body mass in seasons corresponding to when the dominant columnar cacti (e.g., *P. pringlei*) are in flower and fruit in the region (March to July). Male bats were scored as reproductively active if their testes were swollen and distended

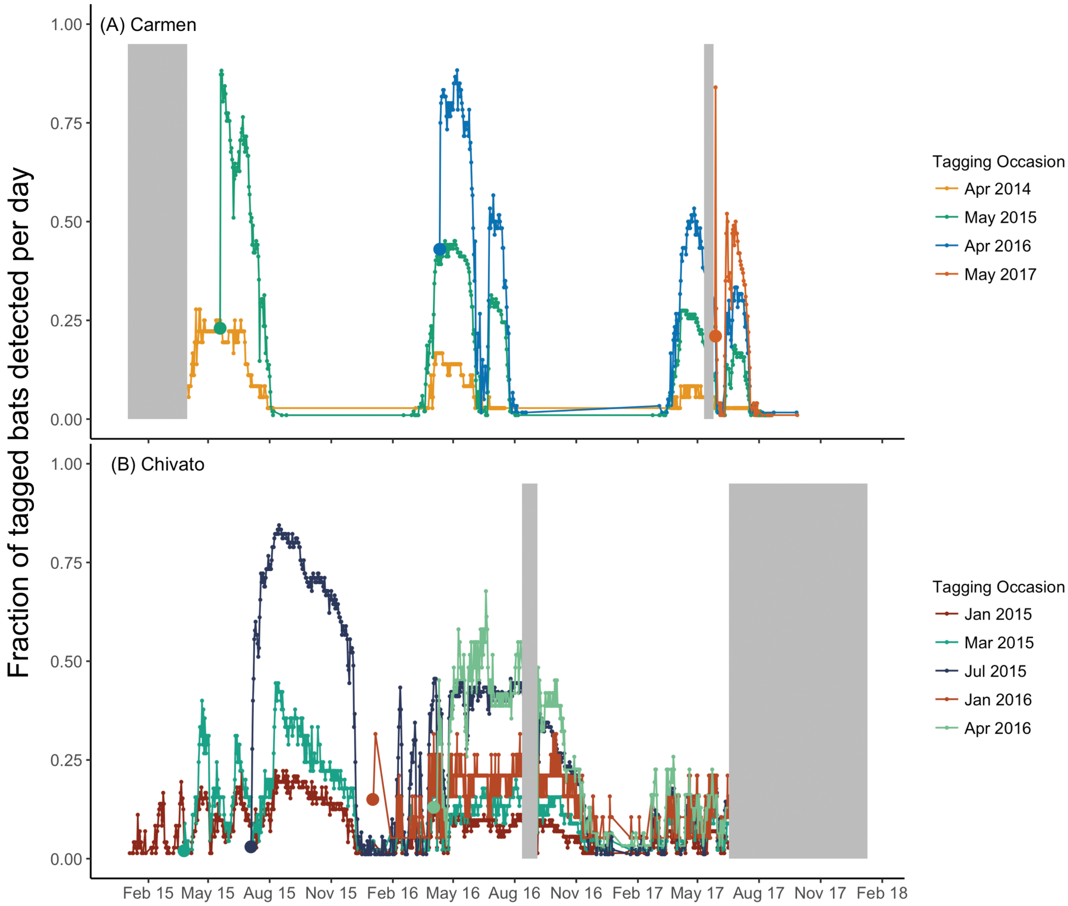

Fig. 3.—Patterns of seasonal occupancy at the Isla Carmen maternity roost in mid-Baja (A) and the Chivato maternity and mating roost in southern Baja (B) from daily detections of bats marked with pit tags passing through antennae at roost entrances. Gray boxes indicate periods when the tag reader was not functioning.

(Racey 1988; Ceballos et al. 1997; Stoner et al. 2003). Male lesser long-nosed bats develop a sebaceous patch in the interscapular dorsal region during mating season (Nassar et al. 2008; Rincón-Vargas et al. 2013). We noted presence of this distinctive patch as well as discolored fur in the middorsal area indicating recent molting and regrowth of fur from a sebaceous patch (Nassar et al. 2008).

Results

Distributional records and roost status.—We report a total of 13 roost sites of lesser long-nosed bats on the Baja peninsula, including discovery of 10 roosts not previously reported in the literature (Table 1). Eight of these roosts were visited in multiple seasons as part of this study (Fig. 1). We discovered 2 predominately male roosts in the southern peninsula (Las Cuevas and Chivato Mine; Fig. 1) and confirmed males were in mating condition at these roosts in autumn, documenting evidence of mating sites for lesser long-nosed bats on the Baja peninsula. We documented the intentional destruction or natural collapse of 3 maternity roosts of lesser long-nosed bats, representing a loss of almost one-third of the known maternity roosts of the species on the peninsula (Table 1).

Seasonal occupancy.—Probability of roost occupancy differed among seasons on the Baja peninsula, but there was not strong support for regional differences in seasonal patterns of roost occupancy (Tables 3 and 4). Occupancy in winter was significantly lower than in spring or summer ($P < 0.04$) in both regions (Fig. 2). Three sites in close proximity to each other (< 15 km) in the Sierra Cacachilas in the southern peninsula had bats present in some winters: 2 sites used as maternity roosts (Azedon, La Gitana) had less than 100 bats present (< 1% of their spring population) and the Chivato roost used for maternity and mating had between 10 and 1,000 individuals in winter (numbers varied by 2 orders of magnitude depending on year but was always < 10% of its spring–summer–fall population; Figs. 2 and 3).

Bats marked with pit tags were detected daily at the Carmen maternity roost from mid-March to mid-July (Fig. 3A), closely corresponding to the seasonal phenology of flowering and fruiting of cardón cacti (Fleming et al. 2001). In contrast, tagged bats were detected nearly year-round at the Chivato roost, although very few bats were detected from November to mid-February (Fig. 3B). At both sites, daily detections of tagged bats were substantially higher in the season they were initially tagged than in following seasons. At Chivato, the fraction of daily detections was consistently lower for bats tagged during January, suggesting the majority of bats using the site during mid-winter migrate elsewhere in other seasons (Fig. 3B).

Reproductive timing and body mass of females.—Timing of parturition at maternity colonies occurred significantly earlier in the year at southern compared to mid-peninsular regions (Fig. 4). In early April, the proportions of newborn and infant stage classes and proportion of females still pregnant were significantly higher ($P < 0.001$) in the mid-peninsula than in the southern peninsula (Table 5; Fig. 4). Conversely, in early April the proportions of pre-volant and volant young and adult females who were lactating were significantly higher ($P < 0.001$) in the south than the mid-peninsula (Table 5; Fig. 4). Young were

Table 4.—Estimated model coefficients and *SE*s for 2 top-ranked models based on Akaike's information criteria (AIC) model selection for seasonal roost occupancy of lesser long-nosed bats (*Leptonycteris yerbabuenae*) on the Baja California peninsula. Although the model with region had competing support based on AIC, the regional term was not significant ($P = 0.41$).

Model term	Coefficient	*SE*	*Z*-value	*P*-value
Pr(Occupancy) ~ season				
Intercept (reference = winter)	−0.96	0.79	−1.21	0.23
Season: spring	3.79	1.73	2.19	0.03
Season: summer	3.66	1.75	2.09	0.04
Season: autumn	1.41	1.07	1.31	0.19
Pr(Occupancy) ~ season + region				
Intercept (reference = winter and southern)	−0.72	0.81	−0.88	0.38
Season: spring	3.77	1.71	2.20	0.03
Season: summer	3.68	1.74	2.12	0.03
Season: autumn	1.42	1.09	1.30	0.19
Region: mid-peninsula	−0.93	1.12	−0.83	0.41

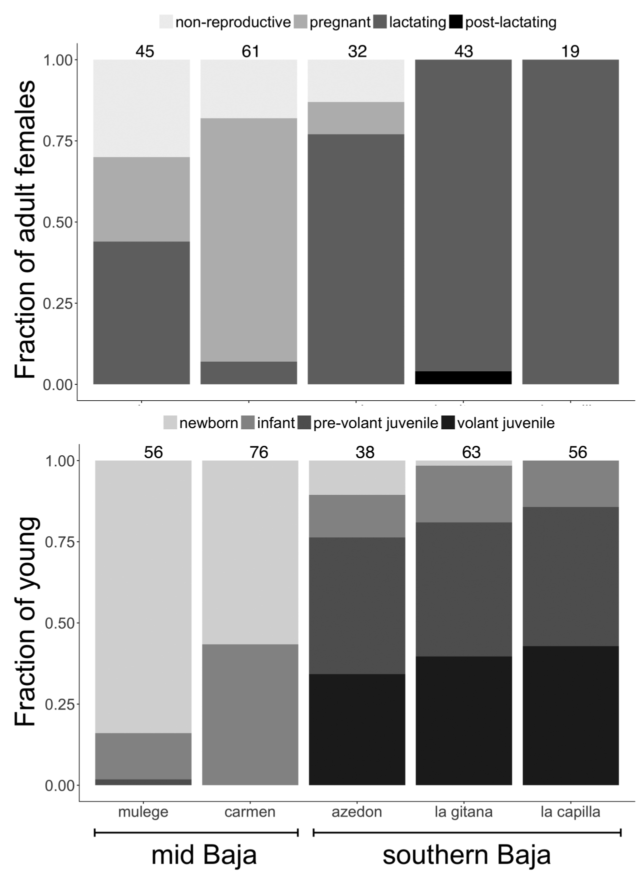

Fig. 4.—Proportion of reproductive and age classes sampled in early April at 5 maternity sites of lesser long-nosed bats (*Leptonyteris yerbabuenae*) on the Baja California peninsula. The proportion of pregnant females and young that were newborn or infants was significantly higher in the mid-peninsular region than in the south (Table 3), suggesting that timing of parturition occurred later at sites in the mid-peninsula compared to the southern peninsula.

Table 5.—Estimated model coefficients and *SE*s for logistic regression models fit to test whether reproductive timing differed by region for lesser long-nosed bats (*Leptonycteris yerbabuenae*) on the Baja California peninsula. Models were fit for each reproductive class (pregnant, lactating) or development stage of young (newborn, infant, pre-volant juvenile, volant juvenile). All models were fit with a binomial distribution and a logit link using a bias-reduction method implemented in the brglm function from package brglm in program R.

Model	Coefficient	*SE*	*Z*-value	*P*-value
Adult females				
Pr(Pregnant) ~ region				
Intercept (reference = southern)	−3.07	0.55	−5.82	< 0.001
Region: mid-peninsula	3.26	0.58	5.82	< 0.001
Pr(Lactating) ~ region				
Intercept (reference = southern)	2.12	0.37	5.79	< 0.001
Region: mid-peninsula	−3.36	0.43	−7.73	< 0.001
Young-of-the-year				
Pr(Newborn) ~ region				
Intercept (reference = southern)	−3.32	0.43	−7.63	< 0.001
Region: mid-peninsula	4.08	0.47	8.61	< 0.001
Pr(Infant) ~ region				
Intercept (reference = southern)	−1.69	0.22	−7.69	< 0.001
Region: mid-peninsula	0.90	0.29	3.12	< 0.01
Pr(Pre-volant) ~ region				
Intercept (reference = southern)	−0.32	0.16	−1.97	0.05
Region: mid-peninsula	−4.15	0.84	−4.95	< 0.001
Pr(Volant) ~ region				
Intercept (reference = southern)	−0.42	0.16	−2.60	< 0.001
Region: mid-peninsula	−5.16	1.4	−3.6	< 0.001

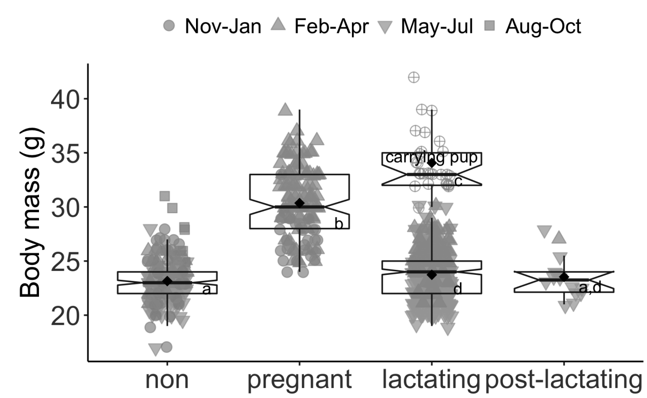

Fig. 5.—Differences in body mass of female lesser long-nosed bats (*Leptonycteris yerbabuenae*) on the Baja California peninsula. Lactating females that were weighed carrying pups are shown as a separate group. Boxplots are notched to show median and quartiles, and black diamonds show means. Letters denote groups that were significantly different based on Tukey's method for post hoc contrasts.

observed starting in mid-February in the south, about 2 months earlier than at mid-peninsula sites.

Pregnant females captured between February and April weighed an average 31 g (*SE* = 0.23), which was an average 37% greater body mass compared to nonreproductive females captured in those months (Fig. 5). Females captured and weighed carrying pups were 10 g (*SE* = 0.46) heavier than lactating females without pups (23.7 g, *SE* = 0.12), demonstrating that females were capable of carrying young weighing 44% of their own body mass. We note that we only captured females

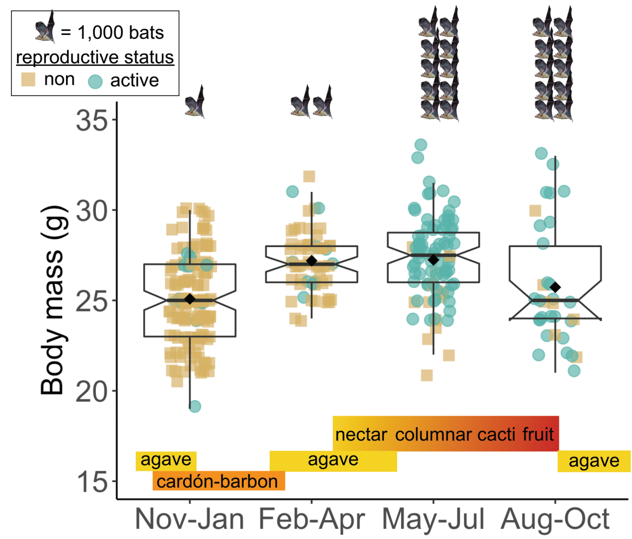

Fig. 6.—Changes in body mass across seasons for male lesser long-nosed bats (*Leptonycteris yerbabuenae*) in the southern Baja California peninsula, Mexico. Males were scored as reproductively active if testes were distended and swollen. Boxplots are notched to show median and quartiles, and black diamonds show means. Letters denote groups that were significantly different based on Tukey's method for post hoc contrasts. Seasonal changes in relative colony size for the Chivato mating roost are shown at top.

carrying young inside a roost or moving to a nearby night roost, indicating females do not likely carry young while traveling long distances during foraging bouts.

Seasonal variation in body mass and reproductive status of males.—Body mass of male lesser long-nosed bats peaked in spring and summer months, coinciding with availability of columnar cacti nectar and fruit availability (Fig. 6). Male bats weighed an average of 27 g in February–April and May–July (Fig. 6), which was 2 g heavier than the average weight of males (25 g) in August–October and November–January. The 2 g increase in body mass from autumn and winter to spring and summer indicates an 8% increase in body mass across seasons. Although adult males with distended and swollen testes were captured in all seasons, there were clear seasonal patterns to reproductive status of males in the southern peninsula. Ninety-four percentage of adult males captured in July had distended and swollen testes (*n* = 65/69) compared to only 10% (*n* = 13/128) captured during mid-winter (December–January; Fig. 6). Almost all adult males captured in early October at Las Cuevas (*n* = 9/10) in 2013 and 61% of adult males captured at Chivato in September 2017 (*n* = 11/18) had active sebaceous patches (bare dorsal skin with sticky fur). About one-half the adult males (*n* = 6/15) captured in mid-October at Chivato in 2016 had bare dorsal skin with regenerating fur suggestive of just finishing mating. In mid-winter visits to Chivato from 2014 to 2016, nearly 43% of adult males captured (*n* = 55/128) had newly grown fur that was distinct in coloration in the area where the dorsal sebaceous patch forms, suggesting these males had been in breeding condition in previous months.

Discussion

We provide evidence of an extensive population of lesser long-nosed bats on the Baja peninsula that is primarily seasonally migratory and includes at least 2 mating sites with males in active breeding condition in the southern peninsula. We found that most female lesser long-nosed bats present on the Baja peninsula use it during the spring and summer to give birth and raise young, a seasonal pattern similar to migratory maternity roosts studied in the northern mainland Sonoran Desert and southwestern United States (Rojas-Martínez et al. 1999). However, some females arrived to give birth at maternity sites in the southern peninsula by mid-February, which is about 2 months earlier than in mid-Baja and northern Sonoran Desert regions. A mating roost in the southern peninsula retained small numbers of both males and females, including some pregnant females, during mid-winter. Except for this small population, lesser long-nosed bats were largely absent from all maternity sites on the Baja peninsula during mid-winter in both the southern and mid-peninsular regions. Our data suggest that the majority of the population of lesser long-nosed bats on the Baja peninsula, including both males and females, migrate over the Gulf of California to the Mexican mainland rather than overwinter in the southern peninsula as had been previously suggested.

The presence of winter-blooming agaves in the southern peninsula has been suggested as a food resource for lesser long-nosed bats that overwinter in the Cape region of Baja (Fleming et al. 1993). While there are 22 species of agave that occur on the Baja peninsula, only 3 species are found in the southern peninsular Cape region (Webb and Starr 2015). Two of these species typically bloom in the spring months from roughly February to April and the other has a typical autumn bloom period from September to December (Rebman and Roberts 2012). Flowering seasons of agaves are more variable and less seasonally predictable than those of columnar cacti and are likely highly influenced by climatic events, such as droughts or hurricanes (R. H. Webb, University of Arizona, pers. comm.). The unpredictability of agave flowering and overall low density of agaves in the region make it unlikely that agaves provide a reliable or substantial food source for a large population of lesser long-nosed bats during winter months in southern Baja. Our data show that the population of lesser long-nosed bats in Baja swells significantly when columnar cacti are flowering and fruiting and only a small fraction of that population remains in the area during mid-winter when nectar and fruit resources are at their lowest availability. Both males and females leave the region when resources are scarce. However, surprisingly, we found that some females began arriving at a few of the maternity sites in the southern peninsula in late stages of pregnancy to give birth by mid-February, which is 2 months earlier than when parturition typically occurs at more northern sites and before the onset or peak of flowering of cardón cacti. Two agave species and the cardón-barbón (*P. pecten-aboriginum*), a columnar cactus restricted to the eastern cape of Baja, bloom during February (Rebman and Roberts 2012), which may provide enough floral resources for a shift in birthing phenology at sites in the southern peninsula.

The seasonal ecology of lesser long-nosed bats appears to be primarily driven by the flowering and fruiting season of the cardón, the dominant columnar cactus on the peninsula (Rebman and Roberts 2012). Parturition was synchronous and timed with onset of flowering at mid-peninsular roosts and although some females arrived in mid-February to southern roosts, there was a second birthing pulse during onset of flowering of cardón at those sites as well (Fig. 4). Body mass of males increased on average by 8% during the flowering and fruiting season of cardón and males had obvious ample fat reserves by July. Although we could not test for seasonal effects on body mass of females due to the confounding effects of pregnancy on body mass during spring, we note that females showed up to maternity sites on the Baja peninsula in mid- to late stages of pregnancy, a period when females are carrying a nearly 40% increase in mass. Arriving from migration in late pregnancy suggests females will be at peak energetic demand when they arrive at maternity roosts and shifts in flowering phenology or availability of dominant food resources could pose risks to these populations (Memmott et al. 2007).

Daily detections of marked bats at pit tag readers at the Carmen and Chivato roosts revealed differences in seasonal use and patterns of behavior. At Carmen, bats arrived synchronously in March and departed synchronously in early August, with no bats present until the following March. In addition, in both 2016 and 2017, the majority of tagged bats departed the roost for about 2 weeks in early June. Early June coincides with when the flowering season of the cardón has largely ended but the majority of fruit are not yet ripe (W. F. Frick, pers. obs.). This may be when resource availability is shifting and bats begin exploring new areas. In contrast, the Chivato roost had some bats present year-round in most years, although occupancy was highest from mid-February to mid-November. Bats departed en masse from Chivato in November 2015, but less synchronously in 2016.

Bats tagged at the Carmen roost showed high fidelity and typically > 75% of tagged bats were detected using the site each day in the same season they were tagged. At Chivato, comparable levels of same-season fidelity were only observed for male bats tagged in July 2015. A few factors could influence lower fractions of daily detections of tagged bats at Chivato. Firstly, Chivato is located very near 2 maternity roosts (< 1 km from La Gitana and < 15 km from Azedon), so bats can easily switch roosts on a nightly basis. We deployed an additional reader at the La Gitana roost entrance in January 2017 and preliminary data suggest roost switching is very common with both male and female bats routinely moving back and forth between the sites. Moreover, patterns of daily detections differed for bats tagged in different seasons and less than a quarter of bats tagged in January used the site consistently, suggesting that the majority of bats using Chivato in mid-winter are not resident year-round but are instead likely migrants.

Lesser long-nosed bats are particularly vulnerable to disturbance at roosts given that they roost in large aggregations in caves and mines (Medellín 2009; Medellín et al. 2017). Protection of maternity sites is a critical conservation strategy for the species and is generally needed for conservation of cave-dwelling bats (USFWS 1995; Medellín et al. 2017). Many of the roost sites we studied on the Baja peninsula are unprotected and vulnerable to future and current disturbance. During our surveys, we discovered 3 maternity roost sites (nearly 1/3 of known maternity sites) were destroyed, 1 by natural causes and the other 2 by deliberate action. The Tesoro mine, which held roughly 10–20,000 lesser long-nosed bats as well as substantial numbers of California leaf-nosed bats (*Macrotus californicus*) and Mexican funnel-eared bats (*Natalus mexicana*), likely collapsed during an earthquake in September 2015 (Table 1). The earthquake occurred at night and it remains unknown how many bats may have been killed as a result. A mine on Isla San Jose that held thousands of lesser long-nosed bats and hundreds of California leaf-nosed bats in May of 2006 was bulldozed and closed. We were unable to obtain details as to when the shaft was closed but if it occurred during April–June, it is likely that thousands of bats were killed as a result. Similarly, the La Capilla roost that was a maternity colony for 4 species, including lesser long-nosed bats, Mexican funnel-eared bats, ghost-faced bats (*Mormoops megalophylla*), and California leaf-nosed bats (Table 1), was bulldozed closed sometime in 2017. In April 2018, we confirmed that an additional roost known by PC-C near the university campus in La Paz (Cueva de la Iglesia; Table 1) had been vandalized with use of fire and the bats had abandoned the site. Conservation efforts to inform locals residing nearby substantial roosts of lesser long-nosed bats and other cavernicolous bat species could help reduce human–wildlife conflicts and support protection of these colonies as has been successful in other parts of Mexico (Medellín 2003, 2009; Medellín et al. 2004). Most remaining known maternity colonies in the southern peninsula occur on a private ranch that is committed to the protection of the bats.

Although the Baja peninsula is separated from mainland Mexico by the Gulf of California, habitats on the Baja peninsula support an extensive population of lesser long-nosed bats that is primarily seasonally migratory and closely linked to the seasonal phenology of columnar cacti. Genetic analyses support that lesser long-nosed bats on the Baja peninsula are connected and that the population expanded into the Baja peninsula following the Pleistocene when food resources became available (Ramirez 2011; Arteaga et al. 2018). Overall, our data support the decision to delist the lesser long-nosed bat from endangered and threatened status in both the United States and Mexico. However, we note that legally and effectively protecting roost sites from deliberate destruction and monitoring populations, including those on the Baja peninsula, will be critical for ensuring the continued persistence of the species. Habitats on the Baja peninsula are at high risk of environmental change both from land use and climate change (Zamora-Gutierrez et al. 2018), and migratory nectar-feeding bats are particularly vulnerable to global changes that affect availability and predictability of seasonal nectar and fruit resources (Medellín et al. 2004; Medellín 2009).

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Photographic key to visual classification of developmental stage class of young-of-year lesser long-nosed bats (*Leptonycteris yerbabuenae*).

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