UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE CIENCIAS

ECOLOGÍA

DEMOGRAFÍA COMPARADA DE TRES ESPECIES DE LAGARTIJAS DEL GÉNERO *SCELOPORUS*: MIGRACIÓN TEMPORAL Y CAMBIOS A CORTO PLAZO EN LA ABUNDANCIA POBLACIONAL.

TESIS

POR ARTÍCULO CIENTÍFICO TITULADO:

POPULATION DYNAMICS OF THREE LIZARD SPECIES FROM THE GENUS *SCELOPORUS*: SHORT-TERM CHANGES IN DEMOGRAPHIC PARAMETERS

QUE PARA OPTAR POR EL GRADO DE:

MAESTRA EN CIENCIAS BIOLÓGICAS

PRESENTA:

SELENE VARGAS GARCÍA

TUTOR PRINCIPAL DE TESIS:
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UNAM POSGRADO
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FACULTAD DE CIENCIAS
DIVISIÓN ACADÉMICA DE INVESTIGACIÓN Y POSGRADO

OFICIO FCIE/DAIP/0022/2019
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M. en C. Ivonne Ramírez Wence
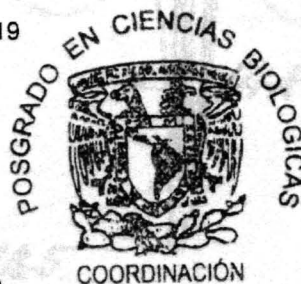**Directora General de Administración Escolar, UNAM**
Presente.

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **15 de octubre del 2018** se aprobó el siguiente jurado para el examen de grado de **MAESTRA EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **Ecología** de la alumna **VARGAS GARCÍA SELENE** con número de cuenta **303165754** por la modalidad de graduación de tesis por artículo científico titulado: **"Population dynamics of three lizard species from the genus *Sceloporus*: short-term changes in demographic parameters"**, el cual fue producto del proyecto realizado en la maestría que lleva por título **"Demografía comparada de tres especies de lagartijas del género *Sceloporus*: migración temporal y cambios a corto plazo en la abundancia poblacional"** realizado bajo la dirección del **DR. JOSÉ JAIME ZÚÑIGA VEGA** quedando integrado de la siguiente manera:

Presidente:	DR. VÍCTOR HUGO REYNOSO ROSALES
Vocal:	DR. SERGIO IVÁN ANCONA MARTÍNEZ
Secretario:	DR. RODRIGO MACIP RÍOS
Suplente:	DR. ANÍBAL HELIOS DÍAZ DE LA VEGA PÉREZ
Suplente:	DR. MANUEL FERIA ORTIZ

Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
"POR MI RAZA HABLARA EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 14 de enero de 2019

DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA

POSGRADO EN CIENCIAS BIOLOGICAS
COORDINACIÓN

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RESUMEN

Los estudios demográficos nos permiten conocer los cambios cuantitativos que suceden en las poblaciones naturales. Identificar el momento exacto dentro del año en el que las tasas vitales cambian drásticamente, nos permite inferir los posibles procesos biológicos o ecológicos responsables. En este estudio, caracterizamos demográficamente a tres especies de lagartijas del género *Sceloporus* que habitan en el centro de México: *S. torquatus, S. grammicus* y *S. megalepidurus*. Registramos datos de captura, marcaje y recaptura durante aproximadamente un año y medio y estimamos en una escala mensual las tasas de supervivencia, reclutamiento, migración temporal, recaptura, así como la tasa de crecimiento poblacional, abundancia y densidad poblacional. Analizamos los datos de captura, marcaje y recaptura en el Programa MARK que utiliza procedimientos de máxima verosimilitud para estimar los parámetros demográficos. Encontramos que durante la temporada con mayores restricciones térmicas (seca-fría) la supervivencia de *S. torquatus* disminuye notablemente. También detectamos un aumento considerable de la tasa de reclutamiento de *S. grammicus* en la época de lluvias (junio-octubre), cuando estas lagartijas están estableciendo territorios y buscando parejas. En contraste, no encontramos evidencia de cambios intra-anuales en la tasa de emigración temporal. Detectamos también que los cambios entre estaciones en la abundancia y la tasa de crecimiento poblacional de las tres especies son consistentes con las variaciones intra-anuales en las tasas de supervivencia y reclutamiento. Este estudio representa una contribución significativa al conocimiento de la variación demográfica intra-anual en especies de lagartijas del género *Sceloporus*.

ABSTRACT

The demographic studies help us to know about the qualitative changes that happen in the natural populations. The identification of the exact moment of the year in which the vital rates have a drastical change, help us to infer the possible biological or ecological processes responsible of it. In this study, we characterize demographically three species of lizard of the genus *Sceloporus* that live in the center region of Mexico: *S. torquatus, S. grammicus* y *S. megalepidurus*. We take the capture, marking and recapture data during a year and a half approximately and then we make a monthly estimation of the surviving, recruitment, temporary migration, recapture rates, and also the population growth, abundance and population density rates. We also analyze the capture, marking and recapture data with MARK program, which uses the procedure of maximum likelihood in order to estimate the demographic parameters. We find that during the season with more thermal restrictions (dry cold) the survival of *S. torquatus* decreases notably. We also detect a considerable increase of the recruitment rate of *S. grammicus* in the rainy season, when these lizards are establishing territory and looking for a couple. By contrast, we do not find evidence of intra-annual changes in the temporary migration rate. We also find that the changes between seasons of abundance and population growth rates of the three species are consistent with the intra-annual variations of the surviving and recruitment rates. This study represents a significant contribution to the knowledge of the intra-annual demographic variation in the lizard species of the Sceloporus genus.

INTRODUCCIÓN

La ecología de poblaciones estudia el tamaño, estructura y dinámica de una población. El principal objetivo de la ecología de poblaciones radica en conocer cuáles son los procesos demográficos responsables de la variación del tamaño poblacional tales como los nacimientos, muertes, inmigraciones y emigraciones (Barlett, 1960; Bailey, 1964; Pulliam, 1988). A lo largo de los años se han realizado una gran cantidad de estudios demográficos que se enfocan en la variación entre años de parámetros demográficos como la supervivencia, la fecundidad y la abundancia poblacional (Dugger et al. 2004; LaManna et al. 2012; Richard et al. 2014). Este tipo de estudios nos permiten conocer el comportamiento y las tendencias cuantitativas de las poblaciones a largo plazo, sin embargo, no nos permiten saber en qué momento particular dentro de un ciclo anual, los parámetros demográficos cambian de manera significativa (Grosbois et al. 2008).

Existe un número considerable de estudios a largo plazo que documentan los cambios demográficos y su relación con las condiciones climáticas durante los años de estudio (Paxton et al. 2014; Havemann et al. 2016). De esta manera, estos trabajos buscan asociar los factores abióticos que se presentaron durante los años de muestreo con aumentos en la mortalidad o disminuciones en la abundancia poblacional (Wang et al. 2009; Wright et al. 2009). No obstante, estos censos inter-anuales no nos permiten conocer el momento específico del año en el que tienen lugar los procesos biológicos como la emigración o la reproducción y que podrían estar relacionados con las variaciones de las tasas vitales.

A pesar de que la información que nos ofrecen este tipo de estudios es valiosa, no es posible saber si la época reproductiva o el invierno están relacionadas con una mayor

mortalidad. En consecuencia, hay una necesidad de censos estacionales o mensuales que documenten el momento específico del año en el que los procesos biológicos o ecológicos tengan lugar y puedan estar relacionados con la variación en las tasas vitales (Dickman et al. 1999; Grosbois et al. 2008; Levy et al. 2015; Zúñiga-Vega 2011).

En reptiles, podemos encontrar estudios que relacionan parámetros demográficos como la abundancia o la supervivencia con las condiciones climáticas en una escala inter-anual (e.g., Salvidio y Oneto 2008; Loehr 2010). Específicamente en lagartijas, existen estudios inter-anuales que intentan relacionar algún factor biótico o abiótico con un aumento o disminución en algún parámetro demográfico. Los factores como la temperatura y la precipitación afectan a los organismos ectotérmicos, de manera que en años en los que aumenta alguno de estos factores se generan cambios drásticos en la supervivencia o en la natalidad (Read et al. 2012: Flesch et al. 2017). Los estudios con especies de lagartijas que se han realizado a una escala menor (i.e., mensual o estacional) y que nos permiten asociar factores bióticos o abióticos (tales como la temperatura, la precipitación, la disponibilidad de alimento y las estaciones reproductivas) con la variación en las tasas vitales son pocos en comparación con los estudios inter-anuales (Wolf et al. 2014; Ujvari et al. 2015).

El género *Sceloporus* (Squamata: Phrynosomatidae) tiene aproximadamente 80 especies, de las cuales 70 se distribuyen desde Estados Unidos hasta Panamá y 30 son vivíparas (Sites et al. 1992; Wiens y Reeder 1997; Martínez-Méndez y Méndez de la Cruz 2007). Este género tiene una gran variación en morfología, patrones de coloración, comportamiento, ecología, historia de vida, dicromatismo sexual y número de cromosomas (Laché y Sites 2010). Lo que lo hace un clado extremadamente diverso y atractivo para estudiar su ecología y evolución. Por esta razón, establecer patrones generales dentro del

género *Sceloporus* posibilita bases sólidas que nos permiten hacer inferencias y respaldar estudios subsecuentes que establezcan la evolución y diversificación del género.

Para lograr nuestro objetivo seleccionamos tres especies de lagartijas pertenecientes al género *Sceloporus* en función de la abundancia, el ciclo reproductivo y la localización geográfica de las poblaciones (ANEXO). Las especies *S. grammicus, S. torquatus* y *S. megalepidurus* son tres especies vivíparas, de reproducción otoñal, localmente abundantes y que habitan el centro de México. Dos de nuestras tres especies de estudio son simpátridas (*S. grammicus* y *S. torquatus*) dentro de nuestras áreas de estudio.

En este estudio, examinamos la tasa de supervivencia, la tasa de reclutamiento, la tasa de migración temporal, la tasa de captura, la tasa de crecimiento poblacional y la abundancia poblacional de tres especies de lagartijas del género *Sceloporus* (*S. torquatus*, *S. grammicus* y *S. megalepidurus*) que habitan el centro de México para determinar la variación en estos parámetros. Para lo cual, realizamos procedimientos de captura, marcaje y recaptura con muestreos de aproximadamente cada tres meses durante un periodo de año y medio. Además de incorporar variables como son el sexo, la estación y la temperatura en el análisis de datos (ANEXO). El objetivo principal de este trabajo fue saber en qué momento del año suceden cambios en la supervivencia, el reclutamiento de nuevos adultos, la emigración temporal y la abundancia poblacional. Así, esta investigación se plantea las siguientes preguntas: ¿Cómo varían los parámetros demográficos de tres especies de lagartijas del género *Sceloporus* a una escala intra-anual? ¿En qué fase del año suceden las variaciones más importantes de las tasas vitales de estas especies? ¿Cuáles son las variables ambientales con las que podemos asociar esta variación?

Los objetivos particulares del trabajo son: (1) conocer las fases específicas del año en las que suceden variaciones en las tasas vitales (supervivencia y reclutamiento). (2) Examinar si la tasa de emigración temporal de estas lagartijas varía a lo largo del año. (3) Saber si las variaciones intra-anuales observadas en las tasas vitales y en la tasa de emigración temporal tienen consecuencias en términos de cambios a lo largo del año en la abundancia poblacional y en la tasa de crecimiento de estas poblaciones. (4) Hacer una comparación cualitativa de los resultados entre las tres especies para tratar de encontrar patrones generales intra-anuales en la dinámica poblacional de lagartijas del género *Sceloporus*.

HIPÓTESIS

Este trabajo tiene como ejes centrales diversas hipótesis. Cada una de éstas, se refiere a un parámetro demográfico particular. En primer lugar, debido a que las lagartijas son organismos ectotermos cuyo metabolismo y comportamiento depende de las temperaturas ambientales (Chamaillé-Jammes et al. 2006; Angilletta et al. 2010; Le Galliard et al. 2010; McKay y Phillips 2012) y a que durante la estación seca y fría se presentan severas restricciones térmicas para estos animales, entonces habrá una disminución en la supervivencia de las tres especies y, como consecuencia, la abundancia poblacional también se verá afectada negativamente durante esta temporada.

En segundo lugar, debido a que en las tres especies la época de apareamiento sucede al final de la época de lluvias y a que los adultos inician la búsqueda y establecimiento de territorios y parejas potenciales un poco antes de que tengan lugar las cópulas (Calsbeek y

Sinervo 2002; Cooper y Vitt 2002; Smith y Lemos-Espinal 2005), el mayor reclutamiento de nuevos individuos reproductivos sucederá justo antes de la época de apareamientos, es decir, durante la temporada lluviosa. Por lo tanto, esperamos también un aumento en la abundancia poblacional durante la época de lluvias debido a la inmigración y al reclutamiento.

En tercer lugar, con respecto al movimiento de los individuos, la tasa de emigración temporal se refiere a la probabilidad de que un individuo se encuentre fuera del área de estudio (i.e., no disponible para su captura) durante alguna temporada y que regrese posteriormente (Pollock et al. 1990; Kendall et al. 1997). Por lo tanto, los individuos que realizan sus actividades en un área pequeña tienen una baja probabilidad de encontrarse fuera del área de estudio durante algún censo particular. Por el contrario, los individuos que tienen mayores áreas de actividad, tienen una alta probabilidad de encontrarse fuera del área de estudio durante algún censo particular. Durante la mayor parte de la estación de secas cálidas los machos de estas tres especies de lagartijas no se encuentran reproductivos (Godínez-Cano 1985; Feria-Ortiz et al. 2001; Ramírez-Bautista et al. 2012) y, por lo tanto, no están estrictamente asociados a territorios. Además de que en esta época seca y caliente hay menor abundancia de alimento (i.e., invertebrados; Ramírez-Bautista y González-Romero 2002) y machos y hembras deben desplazarse más para encontrar presas. Por lo tanto, debido a que el mayor desplazamiento espacial de los individuos debe suceder durante la estación seca cálida, la tasa más alta de emigración temporal sucederá durante esta estación.

Population Dynamics of Three Lizard Species from the Genus *Sceloporus*: Short-Term Changes in Demographic Parameters

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Abstract.—**Most demographic studies focus on numerical changes that occur within populations among years. However, studies at an inter-annual scale do not provide information on the particular times of the year (particular months or seasons) when rates of survival, recruitment, or migration increase or decrease due to physiological, behavioral, or ecological processes. In this study, we collected capture-mark-recapture data on three species of lizards of the genus *Sceloporus* (*S. torquatus*, *S. grammicus* and *S. megalepidurus*) found in ecologically similar habitats to examine potential changes in demographic rates among three different climatic seasons: rainy, cold-dry, and warm-dry seasons. We tested different hypotheses about the effect of these three seasons of the year on survival, recruitment of new adults, and temporary emigration. We found that during the season with severe thermal constraints, the cold-dry season, survival of *S. torquatus* decreased markedly. We also detected a considerable increase in the recruitment rate of *S. grammicus* during the rainy season, when these lizards are establishing territories and finding mates. In contrast, we found no evidence of intra-annual changes in the rate of temporary emigration. In addition, we calculated abundance and population growth rate for each species and for each season. Our study represents a significant contribution to the understanding of intra-annual demographic variation in lizards.**

Key Words.—Abundance; recruitment; sceloporine lizards; survival; temporary emigration

INTRODUCTION

Most demographic studies aim to understand inter-annual variation in population parameters such as survival and abundance (Oro et al. 2010; LaManna et al. 2012; Sandvik et al. 2012). Even though yearly estimates are important, inter-annual studies do not provide information on the specific times of the year during which critical demographic events occur (Grosbois et al. 2008). For example, there is a considerable number of studies on birds documenting years in which both survival and abundance decrease dramatically (e.g., Sillett et al. 2000; Wright et al. 2009; Paxton et al. 2014; Ancona et al. 2017). These studies attempt to identify the causes of these decreases through correlations between their demographic estimates and the average climatic conditions of their studied years. However, these annual censuses do not provide information on the times of the year (e.g., seasons) when critical processes like emigration or reproduction occur, which may be responsible for the observed decreases in survival and abundance. In mammals, several long-term studies document years with drastic reductions in population density (e.g., Owen-Smith et al. 2005; Wang et al. 2009; Havemann et al. 2016). However, at this scale it is not possible to distinguish if mortality increases during specific periods, such as the reproductive season or the winter. Therefore, studies based on monthly or seasonal censuses are required in order to determine the times of the year when critical biological or ecological processes lead to changes in the vital rates (Grosbois et al. 2008; Levy et al. 2015).

In lizards, there are studies that analyze inter-annual variation in vital rates, such as fecundity or survival, and relate these variations to some biotic or abiotic factor that could be affecting these demographic parameters (Le Galliard et al. 2010; Pastro et al. 2013; Wolf

et al. 2014; Ujvari et al. 2015). For example, Read et al. (2012) found that survival in four species of the genus *Ctenotus* increases in years with more precipitation. On the contrary, Flesch et al. (2017) found that the abundance of the lizard *Uta stansburiana* decreases in years of increased precipitation. With this type of study, we cannot know at what specific time of the year the effect of precipitation (whether positive or negative) on survival and abundance occurs.

Though less common, there are also some studies on lizards based on censuses conducted on a shorter time scale (i.e., monthly or seasonal), that document within-year variation in demographic parameters. These short-term censuses show that temperature, precipitation, and food availability during particular months, as well as the reproductive season, can notably affect the vital rates of these organisms (Niewiarowski et al. 2004; Endriss et al. 2007; Ramírez-Bautista et al. 2016). For example, Zúñiga-Vega (2011) found that females of *Xenosaurus grandis* have higher mortality during the months which coincide with the late gestation and early postpartum periods. Dickman et al. (1999) observed that the abundance of juveniles of two species of the genus *Ctenophorus* increases considerably during the fall when precipitation from the previous summer was relatively high, apparently because abundant rain favors the survival and growth of the young. Studies at the intra-annual scale on lizards are still needed to understand how biological and ecological processes that vary throughout the year (i.e., climatic and reproductive seasons) affect population parameters of these organisms.

In this study, we examined different demographic parameters in three species of lizards of the genus *Sceloporus* inhabiting central Mexico: *S. torquatus*, *S. grammicus,* and *S. megalepidurus.* We implemented capture–mark–recapture procedures, sampling

approximately every three months. Our main objective was to know during which season of the year changes in survival, recruitment of new adults, temporary emigration and population abundance occur. Specifically, we tested the following hypotheses. First, since lizards are ectothermic organisms whose metabolism and behavior depend on environmental temperature (Chamaillé-Jammes et al. 2006; Angilletta et al. 2010; Le Galliard et al. 2010; McKay and Phillips 2012), we predict a decrease in survival in all three species during the cold-dry season. As a consequence of reduced survival, population abundance should also decrease during this season.

With respect to recruitment of new reproductive individuals, we expect an increase just before the breeding season, because adults initiate the search and establishment of territories and potential mates (Calsbeek and Sinervo 2002; Cooper and Vitt 2002; Smith and Lemos-Espinal 2005). In addition, before the breeding season, new individuals that have just reached sexual maturity also join the search for mates (Ortega-León et al. 2007). In all three species, breeding begins towards the end of the rainy season (Godínez-Cano 1985; Feria-Ortiz et al. 2001; Ramírez-Bautista et al. 2012). Therefore, we expect the highest recruitment of adults to occur during this season. As a consequence of the increase in recruitment of new adults, we expect an increase in population abundance during the rainy season.

In addition, we estimated the rate of temporary emigration, which refers to the probability that an individual is temporarily outside the study area (i.e., not available for recapture) during a particular season, with subsequent return to the study area (Pollock et al. 1990; Kendall et al. 1997). The rate of temporary emigration is therefore determined by the movement of individuals across space. Individuals that carry out their activities within

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a small area have a low probability of being outside the study site during any particular census, whereas individuals that move across longer distances (i.e., that have larger activity areas), have a higher probability of being outside the study area during any particular census. We predict an increase in the movement of individuals and, in consequence, increased temporary emigration, during the warm-dry season for two reasons. First, during most of this season males of the three study species are not breeding (Godínez-Cano 1985; Feria-Ortiz et al. 2001; Ramírez-Bautista et al. 2012) and, therefore, are not strictly restricted to their territories. Second, during the warm-dry season, food (i.e., invertebrates) is less abundant (Ramírez-Bautista and González-Romero 2002) and, therefore, both males and females must move more to find prey.

MATERIAL AND METHODS

Study species.— *Sceloporus torquatus, S. grammicus* and *S. megalepidurus* are all viviparous, insectivorous lizard species inhabiting central Mexico (Sites 1992; Ramírez-Bautista and González-Romero 2002; Leyte-Manrique and Ramírez-Bautista 2010). *S. torquatus* is a saxicolous lizard (Smith 1936; Duellman 1961). Males and females of this species reach sexual maturity at a minimum snout-vent length (SVL) of 73 mm (Feria-Ortiz et al. 2001). Matings occur in the fall (October–November). Vitellogenesis begins at the end of the summer (August – September) and ovulation occurs at the end of November and beginning of December. Females are pregnant over the winter (December – March) and young are born the following spring (April – May) (Feria-Ortiz et al. 2001; Ramírez-Bautista and González-Romero 2002). This species exhibits sexual dimorphism; adult males are larger than females and have large colorful (blue and black) ventral patches.

Females also have colorful patches on their bellies, but these are smaller and less intense than in males (Martínez-Méndez and Méndez-de la Cruz 2007).

Sceloporus grammicus is a predominantly arboreal species (Ramírez-Bautista et al. 2009). Size at maturity is 42.5 mm SVL in males and 40.7 mm SVL in females (Pérez-Mendoza and Zúñiga-Vega 2014). Matings occur in the fall (October – November) (Pérez-Mendoza et al. 2014). Vitellogenesis begins in the summer (July – October) and ovulation occurs between November and December. Females are pregnant during the winter and young are born in early spring (Guillette and Casas-Andreu, 1980; Ortega and Barbault 1984; Ramírez-Bautista et al. 2004, 2005, 2012; Jiménez-Cruz et al. 2005). This species is also sexually dimorphic; males have blue, orange, or yellow patches on their throats and black and blue ventral patches, whereas females lack these patches and can present slightly orange coloration on their bellies (Ramírez-Bautista et al. 2012).

Sceloporus megalepidurus is a species that uses a diversity of plants (yuccas, agaves, cacti) as microhabitat (Smith 1939; Sánchez-Herrera 1980). Males reach sexual maturity at 45 mm SVL whereas females mature at 37 mm SVL (Godínez-Cano 1985; González-Ruiz 1991). Matings also occur in the fall (October–November), vitellogenesis occurs during the rainy season (August – September), ovulation occurs in October and November, females are pregnant over the winter, and young are born in March (Sánchez-Herrera 1980; González-Ruiz 1991). There is no evident sexual dimorphism in this species; both sexes lack color patches on the belly or throat.

Study areas.—We studied these three lizard species at ecologically similar sites. For *S. torquatus*, we worked in the botanical garden that is located within the Pedregal de

San Ángel Ecological Reserve (*Reserva Ecológica del Pedregal de San Ángel*; SEREPSA, 2018) in southern Mexico City (19.31826 N, -99.19431 W). The REPSA has an elevation of 2300 masl. The main vegetation type is xerophytic scrub, dominated by the bush *Pittocaulon praecox* (Feria-Ortiz et al. 2001; Rojo and Rodríguez 2002; Argaez et al. 2018). The study area for *S. grammicus* is located in the vicinity of Nopala de Villagrán, in the state of Hidalgo (20.26834 N, -99.64171 W) at an elevation of 2400 masl. This is a semi-arid region with xerophytic scrub (INEGI 2002; Flores-Villela and Canseco-Márquez 2007; Gómez-Mendoza 2007; Roth-Monzón et al. 2018). The study area for *S. megalepidurus* was the area around Lake Alchichica (19.40568 N and -97.40240 W), located in the state of Puebla at an altitude of 2436 masl (Hernández-Márquez 2016). The predominant vegetation is xerophytic scrub, with plants belonging to the genera *Agave*, *Opuntia*, *Dasylirion*, and *Nolina* (González-Ruiz 1991; Alcocer et al. 2000; Rzedowski 2006). In all three study sites, the rainy season occurs from June through October and the dry season from November through May.

Field methods.—In the three study areas, we delimited a plot of approximately one ha in which we captured adult males and females by hand or noose. In the REPSA botanical garden, we sampled *S. torquatus* nine times (an average of once every two months) between August 2015 and March 2017. In Nopala de Villagrán, we sampled *S. grammicus* seven times (on average every three months) between April 2016 and October 2017. In Lake Alchichica we sampled *S. megalepidurus* seven times (on average every 2.5 months) between February 2016 and June 2017. Each sampling period lasted between five and eight consecutive days. Each captured lizard was measured (± 0.01 mm SVL), weighed (± 0.1 g), and individually marked with a unique combination of small scars on the

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ventral surface of the limbs using a medical cautery pen (Ekner et al. 2011, Argaez et al. 2018). We determined the sex of each lizard by the presence (males) or absence (females) of enlarged post-anal scales (Mayhew 1963; Doughty et al. 1994). During each subsequent visit to each site, we recorded the number of recaptured individuals and marked lizards that had not been previously captured.

Mark-recapture analyses.—We analyzed the capture-mark-recapture data using program MARK, which uses maximum likelihood procedures to estimate several demographic parameters (White and Burnham 1999). In all analyses we focused exclusively on adult individuals (i.e., lizards whose SVL was larger than that reported in the literature as minimum length at sexual maturity). We considered that the demographic parameters of these three lizard species could vary drastically among three climatic seasons that clearly differ in temperature and precipitation. The rainy season begins in June and ends in October. We divided the dry season into two periods: the cold-dry season, from November through February, and the warm-dry season, from March through May.

We used Pradel models for open populations (Pradel 1996) to estimate the apparent survival rate (φ), recruitment rate (f), recapture probability (p), and population growth rate (λ). Specifically, the recruitment rate (f) refers to the number of reproductive individuals that enter the population for each adult individual already present in the population. Pradel models allow the estimation of λ as the sum of φ and f (Franklin 2001). In order to implement these Pradel models, we combined data from consecutive daily visits in such a way that, pooled together, these multiple consecutive visits represent a single occasion for each sampling period.

We constructed alternative models representing different hypotheses about variation in φ, f, and p. We considered a null or constant model (.), variation among seasons (e), between sexes (s), an additive effect of sex and season ($s + e$), and a sex by season interaction ($s \times e$). In addition, for recapture probability, we evaluated the effect of average daily temperature (*temp*), an additive effect of temperature and sex ($s + temp$), and a sex by temperature interaction ($s \times temp$). Considering all possible combinations of these sources of variation resulted in a total of 200 models per species.

We selected the best model based on the Akaike information criterion adjusted for small sample sizes (AICc), where the smallest AICc value indicates the model that provides the best fit to the data. However, models that differ by less than two AICc units (ΔAICc < 2) from the best model are also strongly supported by the data (Akaike 1973; Burnham and Anderson 2002). In addition, we calculated AICc weight (w) for each model, which represents a relative measure of the strength of evidence in favor of each model. Based on these AICc weights, we generated weighted averages (across all models) of φ, f, p and λ for each combination of sex and season (Burnham and Anderson 2002).

To estimate population abundance (N) and rate of temporary emigration (γ) we used the robust design of Pollock et al. (1990), in which the sampling scheme consists of primary periods separated by long time intervals (two or three months in our case), which in turn are composed of secondary sampling periods separated by shorter time intervals (consecutive days in our case). During these secondary periods, we assume that the population is demographically closed, allowing the estimation of population abundance. In between the primary sampling periods, the population is open, so additions (births and

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immigration) and subtractions (deaths and emigration) can occur, because they are separated by longer time intervals (Kendall 1999). Therefore, the robust design also allows the estimation of survival (φ) and temporary emigration (γ), as well as recapture probability (p) (Pollock et al. 1990).

The rate of temporary emigration (γ) is defined as the probability that an individual is temporarily outside the study area, and therefore not available for recapture, during a particular primary sampling period. According to Kendall et al. (1995, 1997) this parameter can be expressed in two forms (γ' and γ''). The parameter γ' represents the probability that an individual is not available for capture during a primary sampling occasion (i) given that the animal was not present in the study area during the previous primary sampling occasion (i - 1). On the other hand, γ'' represents the probability that an individual is not available for capture during a given primary sampling occasion (i) given that the animal was present in the study area during the previous primary sampling occasion (i - 1). However, we did not distinguish between these two forms of temporary emigration because when estimating both parameters their standard errors were too large. We therefore decided to set γ' equal to γ'' in all our models.

Using the robust design, we constructed different models to test biological hypotheses with respect to variation in φ, γ and p. Population abundance (N) was calculated as a derived parameter. As in Pradel models, we considered a null model (.), variation among seasons (e), between sexes (s), an additive effect of sex and season ($s + e$), and a sex by season interaction ($s \times e$). In addition, for recapture of probability, we considered the effect of average daily temperature (*temp*), and additive and interactive effects of temperature and sex ($s + temp$ and $s \times temp$, respectively).

Unfortunately, our data were insufficient to appropriately estimate seasonal variation in temporary emigration for two of the three study species: *S. grammicus* and *S. megalepidurus* (i.e., the standard errors estimated for this parameter for different seasons were too large). Therefore, for these two species we only considered a null model and the effect of sex on γ, resulting in a total of 80 models. For *S. torquatus* we did estimate seasonal variation in γ, yielding a total of 200 models for this species.

Once again, we selected the best model based on AICc and calculated weighted averages of φ, γ, p and N for each combination of sex and season, considering the AICc weight (w) of each model (Burnham and Anderson 2002). However, model-averaged estimates of φ and p for each sex and season derived from the robust design models were very similar to these parameters estimated from the Pradel models. Therefore, for simplicity we only report model-averaged survival and recapture rates derived from the Pradel models. However, for *S. grammicus* and *S. megalepidurus* we also report the effect of average temperature per secondary sampling period (i.e., average temperature of each sampling day) on p, given that the best-fitting robust design models included this effect. We report all demographic parameters on a monthly scale.

RESULTS

For *S. torquatus*, we marked a total of 497 adult individuals, of which 297 were females and 200 were males. Of these, we recaptured 141 individuals at least once, of which 90 were females and 51 were males. For *S. grammicus*, we marked a total of 737 adult individuals, of which 422 were females and 315 were males. Of these, 215 individuals were recaptured at least once, of which 118 were females and 97 were males.

For *S. megalepidurus*, we marked a total of 689 adult individuals, of which 362 were females and 327 were males. Of these, 173 individuals were recaptured at least once, of which 93 were females and 80 were males.

Pradel models

Sceloporus torquatus.—The monthly survival rate of *S. torquatus* was notably high (> 0.8 in all cases) and clearly varied among seasons: the three best-supported models (ΔAICc < 2) included the effect of season (Table 1). Although the effect of sex was included in two of the best models, the third of these models with strong support did not include this factor (Table 1). This means that considering differences between males and females in φ did not substantially improve model fit compared to models that only included the effect of season. Survival of both sexes decreased in the cold-dry season and was substantially higher during the rainy season (Fig. 1a).

Season also clearly affected recruitment rate: the three best models included this factor (Table 1). Also in this case, the effect of sex was not entirely evident. Recruitment in males and females was practically zero during the cold-dry season and relatively high (between 0.14 and 0.20) during both the rainy season and the warm-dry season (Fig. 1b). We could not adequately estimate the recruitment rate of females during the rainy season.

As a result of decreased survival and recruitment during the cold-dry season, the rate of population growth for both sexes was statistically less than one during this season (Fig. 1c). On the contrary, λ was greater than one for both sexes during the warm-dry

season and for males during the rainy season, whereas λ for females was statistically equal to one during the rainy season (Fig. 1c).

The three best-supported models indicated an effect of the interaction between sex and season on the recapture probability of *S. torquatus* (Table 1). During the rainy and cold-dry seasons, we did not detect a difference between sexes in *p*, whereas during the warm-dry season, the recapture probability for females was higher than for males (Fig. 1d).

Sceloporus grammicus.—The monthly survival rate of *S. grammicus* was also notably high (> 0.8 in all cases). The three best-supported models included effects of season and sex (Table 1). The top model suggested an additive effect of these two factors and adding the interaction term did not substantially improve model fit (Table 1). However, the weighted averages of φ showed a slight increase in female survival during the cold-dry season and a slight decrease in survival of both sexes during the rainy season (Fig. 2a).

According to the three best-supported models, recruitment of *S. grammicus* clearly varied among seasons without a clear effect of sex (Table 1). This parameter was equal to zero in males and quite close to zero in females during the cold-dry season, with intermediate values during the warm-dry season (0.05 and 0.08 for males and females, respectively) and higher values during the rainy season (0.18 and 0.13 for males and females, respectively) (Fig. 2b). The rate of population growth was statistically less than one only for males during the cold-dry season (Fig. 2c), the season during which recruitment of this sex was equal to zero (Fig. 2b).

The three best-supported models indicated an effect of the interaction between sex and season on the recapture probability of *S. grammicus* (Table 1). During the warm-dry season, we did not detect differences between sexes in *p*. During the rainy season, recapture probability was higher for males, whereas during the cold-dry season recapture probability was higher for females (Fig. 2d).

Sceloporus megalepidurus.—As in the other two species, the monthly survival rate of *S. megalepidurus* was notably high (> 0.85 in all cases). Given that the model with constant survival (null model) had strong support in the data (ΔAICc = 0.06 with respect to the top model), including the effects of sex or season did not improve model fit (Table 1). We thus found little evidence of differences between sexes or among seasons in φ (Fig. 3a).

In contrast, the effects of sex and season were clearly evident in the recruitment rate of *S. megalepidurus* (Table 1). Recruitment was quite close to zero during the rainy and cold-dry seasons, with an evident increase in this parameter during the warm-dry season (Fig. 3b). During this latter season, males had a higher recruitment rate than females (0.32 and 0.19, respectively; Fig. 3b).

The rate of population growth for both sexes was less than one during the cold-dry season (Fig. 3c), when *f* was practically zero (Fig. 3b). On the contrary, during the warm-dry season, λ of both sexes was statistically greater than one (Fig. 3c), which was consistent with the substantial increase in *f* of both males and females during this season. The model with constant *p* (null model) ranked first in this species (Table 1). Therefore, we found no evidence of differences between sexes or among seasons in the recapture probability of *S. megalepidurus* (Fig. 3d).

Robust design models

Sceloporus torquatus.—The model considering a constant emigration rate (null model) ranked first in this species (Table 2). The effect of season had weak support in the data (ΔAICc = 9.34 and w = 0.005 for the first model that included differences among seasons in γ). During all seasons, the proportion of individuals that moved outside the study area was similar between sexes, around 0.4 and 0.5 (Fig. 4a).

In no season did we detect statistical differences between males and females in population abundance. Abundance of females was almost identical during the rainy and warm-dry seasons (around 212 individuals), whereas for males the estimate of N varied between 136 and 177 individuals (Fig. 4b). During the cold-dry season, N decreased notably for both sexes, with approximately 104 females and 85 males (Fig. 4b).

Sceloporus grammicus.—Also in this species, the model considering constant emigration rate had the strongest support (Table 2). For both sexes and all seasons, γ was approximately 0.20 (Fig. 5a).

In *S. grammicus*, we did detect differences between sexes in N during the cold-dry and warm-dry seasons. Abundance of males was lower (between 125 and 161 individuals) than abundance of females (between 319 and 324 individuals) during both seasons (Fig. 5b). During the rainy season we did not find evidence of differences between sexes in this parameter (our estimates were 299 males and 337 females; Fig. 5b).

In the case of recapture probability estimated using the robust design, the three best-supported models included an effect of average daily temperature (Table 2). Adding an

effect of sex did not notably improve the fit of these models and, therefore, p was similar between sexes. Apparently, p of both males and females decreased slightly with increasing average daily temperature (Fig. 5c).

Sceloporus megalepidurus.—As in the other two species, the model considering a constant emigration rate was strongly supported (Table 2). For all seasons, γ was estimated as 0.15 for males and 0.17 for females (Fig. 6a).

Abundance of both sexes notably decreased during the cold-dry season (around 175 males and 301 females), compared to the rainy (around 486 males and 546 females) and warm-dry (around 391 males and 578 females) seasons (Fig. 6b). Similar to *S. grammicus*, the abundance of *S. megalepidurus* females was higher than that of males during the cold-dry and warm-dry seasons (Fig. 6b), although these differences between sexes were not as drastic as in *S. grammicus* (Fig. 5b).

The four best-supported models included an effect of the interaction between average daily temperature and sex on p (Table 2). The estimate of p for males decreased with increasing average daily temperature, whereas p for females was not affected by this environmental variable (Fig. 6c).

DISCUSSION

The analysis of demographic rates at an intra-annual scale allowed us to observe the time of the year when the most drastic changes in survival, recruitment, and abundance occur in our three study species. In addition, we report for the first time in the genus *Sceloporus* estimates of temporary emigration from the study area. Our results demonstrate

interesting differences among the three species, which we discuss in the context of the hypotheses that we proposed for this study.

Hypothesis 1: survival decreases during the cold-dry season

This hypothesis was confirmed only in one of our three study species: *S. torquatus*. Survival of both sexes decreased during the cold-dry season. Temperature has a critical influence on all physiological processes of ectothermic organisms (Huey et al. 2009; Kearney 2013; Abram et al. 2017). In lizards, there is a diversity of studies on the impact of temperature on processes such as digestion, disease resistance, gestation, and activity (Angilletta et al. 2002; Kearney and Porter 2004; Le Galliard et al. 2010; McKay and Phillips 2012). Therefore, drastic reductions in environmental temperature could lead to severe alterations of vital functions such as metabolism and the immune system, which could in turn lead to increased mortality (Angilletta et al. 2004, 2010; Chamaillé-Jammes et al. 2006). Jones and Ballinger (1987) found that only 22% of juveniles of the lizard *Sceloporus undulatus* survive the winter. In the snake *Crotalus viridis*, smaller individuals have lower survival rates during the winter due to physiological costs of hibernation (Ashton 2001). Chamaillé-Jammes et al. (2006) demonstrated that in the lizard *Lacerta vivipara* higher temperatures during spring and summer are directly related to increased survival.

We did not find support for this hypothesis in *S. grammicus* or *S. megalepidurus.* On the contrary, in *S. grammicus* we observed that females have a slightly higher survival rate in the cold-dry season, and in *S. megalepidurus* we found no differences in survival among seasons. These differences from what we observed in *S. torquatus* can be

tentatively explained in two ways. First, decreases in temperature in the microhabitats

occupied by *S. torquatus* may be more intense than those experienced by *S. grammicus* and

S. megalepidurus. The study area for *S. torquatus* is a botanical garden with greater tree

cover, which may lead to increased thermal constraints (i.e., fewer refuges and perch sites

that receive direct sunlight). In contrast, the study sites for *S. grammicus* and *S.

megalepidurus* are xerophytic scrubs, where vegetation is much more open. Second,

increased survival in female *S. grammicus* during the cold-dry season could be due to

differences in behavior compared to the other two species. Even though females from all

three species are pregnant during the winter (González-Ruiz 1991; Ramírez-Bautista and

González-Romero 2002; Jiménez-Cruz et al. 2005;) and during gestation many species of

lizards have lower mobility and forage less frequently (Weiss 2001; Sinervo et al. 2010),

female *S. grammicus* could have the lowest activity levels compared to the other two

species, making them notably less conspicuous to predators.

Hypothesis 2: recruitment increases during the rainy season

Given that matings in all three species begin toward the end of the rainy season, we

proposed the hypothesis that just before matings (i.e., during the rainy season), new adult

individuals should recruit into the population. Both males and females must search for

potential mates and establish territories during the rainy season, which would lead to the

arrival of new adult individuals to the study area. We found support for this hypothesis

only in *S. grammicus*, in which the recruitment rate of both sexes was highest during the

rainy season.

In contrast, the recruitment rate for adults of *S. megalepidurus* was notably lower during the rainy and cold-dry seasons. During the warm-dry season, on the other hand, approximately six months before matings, recruitment in this species was relatively high: 0.19 females for each female present in the population and 0.32 males for each male present in the population. Therefore, in this species recruitment is apparently not associated with the search for mates, but rather could be the result of searching for sites with higher food availability during the driest and warmest time of the year, during which the abundance of potential prey (i.e., invertebrates) is notably low (Ramírez-Bautista et al. 2016). This hypothesis was not supported in *S. torquatus* either. Recruitment of adults in this species was relatively high during both the rainy season and the warm-dry season. Thus, this demographic process is not strictly associated with the pre-mating season in this species either.

Hypothesis 3: temporary emigration increases during the warm-dry season

The rate of temporary emigration is associated with the movement of individuals throughout space. We proposed the hypothesis that the three species of lizards would move more during the non-reproductive season, when they are not restricted to territories, which is the warmest and driest season of the year. This season also coincides with the months during which food availability is lowest, when individuals should have to move the most in order to find prey. The prediction derived from this hypothesis was that the rate of temporary emigration out of the study area would be highest during the warm-dry season. Unfortunately, we were only able to test this hypothesis using the data from *S. torquatus* (due to convergence problems when season was incorporated as a factor affecting the rate of temporary emigration of the other two species). In this species, we did not find evidence

of variation due to season or sex. However, we must notice that the values estimated for this parameter were quite high: on each sampling occasion between 40% and 50% of marked individuals were outside the study area. This is evidence that these lizards move considerable distances throughout the year, independent of the phase of the reproductive cycle.

Our study is the second to estimate this demographic parameter for lizard species. Smith et al. (2012), working with the gecko *Nephrurus stellatus* in Australia, reported a temporary emigration rate of 0.093 (i.e., on each sampling occasion 9.3% of marked individuals were temporarily outside the study area). This estimate of temporary emigration is considerably lower than what we observed in *S. torquatus*, suggesting that this latter species moves around relatively large areas.

Abundance and population growth rate

In general, our results are consistent in terms of the expected effects of seasonal variation in recruitment and survival on population abundance. In *S. torquatus*, reductions in survival and recruitment of both sexes during the cold-dry season lead to decreased abundance and population growth rate during this season. In *S. grammicus* the abundance of males decreased notably during the cold-dry and warm-dry seasons, apparently due to drastic reductions in recruitment during these two seasons. In fact, the population growth rate of males indicates a substantial decrease in the number of adult males during the cold-dry season, when recruitment was practically zero. On the contrary, the increase in female survival during the cold-dry season compensated the decrease in female recruitment during this season, leading to relatively stable abundance and population growth rate throughout

the year for females. At the same time, this generated a female-biased sex ratio in *S. grammicus* during the dry periods of the year. Other studies on lizards have also found that females are more abundant than males, for example in the lizard *Sceloporus scalaris* (Ortega-Rubio et al. 2000) and in the dwarf chameleon *Bradypodion pumilum* (Katz et al. 2013).

In *S. megalepidurus,* both abundance and population growth rate were lowest during the cold-dry season, when recruitment of both sexes was practically zero. During the warm-dry season, individuals of both sexes were recruited into the population, generating positive population growth rates during this season. Also in this species we detected greater abundance of females during both dry seasons compared to the abundance of males. This female-biased sex ratio could have interesting consequences in terms of the intensity of sexual selection (McCoy et al. 2004; Bock et al. 2010). If there are relatively few males, then male-male competition for potential mates should be relaxed, which could reduce the magnitude of sexual size dimorphism (i.e., relatively smaller males; Berns 2013). Consistent with this hypothesis, the most intense sexual size dimorphism occurs in *S. torquatus*, which is the species in which we did not find differences in abundance between males and females and in which males are notably larger than females (Ramírez-Bautista and González-Romero 2002). In *S. grammicus* there is moderate sexual size dimorphism (Jiménez-Cruz et al. 2005) and in *S. megalepidurus* there is no sexual size dimorphism (González-Ruiz 1991).

Finally, our estimates of population abundance indicate that our three study species are locally abundant. If we take into account that the three study sites had an average area of 1 ha, the lowest population density we observed was 85 lizards/ha in *S. torquatus* during

the cold-dry season, and the highest was 578 lizards/ha in *S. megalepidurus* during the

warm-dry season. These densities are relatively high compared to densities of other species

from the same genus, such as *S. undulatus* (63.5 lizards/ha; Buckley et al. 2008), *S. scalaris*

(48 lizards/ha; Ortega-Rubio et al. 2000) and *S. woodi* (5 lizards/ha; McCoy et al. 2004).

LITERATURE CITED

Abram, P.K., G. Boivin, J. Moiroux, and J. Brodeur. 2017. Behavioral effects of temperature on ectothermic animals: unifying thermal physiology and behavioral plasticity. Biological Reviews 92:1859–1876.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pp. 267–281 *In* International symposim information theory. Second edition. Petrov B.N. and F. Cazakil (Eds). Akademiai Kidao, Budapest, Hungary.

Alcocer, J., A. Lugo, E. Escobar, M.R. Sánchez, and G. Villaclara. 2000. Water column stratification and its implications in the tropical warm monomictic Lake Alchichica, Puebla, México. Verhandlungen Internationalis Vereinigung Limnologiae 27:3166–3169.

Ancona, S., F.V. Dénes, O. Krüger, T. Székely, and S.R. Beissinger. 2017. Estimating adult sex ratios in nature. Philosophical Transactions Royal Society B372:20160313.

Angilletta, Jr. M.J., P.H. Niewiarowski, and C.A. Navas. 2002. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology 27:249–268.

Angilletta, Jr. M.J., P.H. Niewiarowski, A.E. Dunham, A.D. Leaché, and W.P. Porter. 2004. Bergmann's clines in ectotherms: illustrating a life-history perspective with sceloporine lizards. The American Naturalist 164:E168–E183.

Angilletta, Jr. M.J., B.S. Cooper, M.S. Schuler, and J.G. Boyles. 2010. The evolution of thermal physiology in endotherms. Frontiers in Bioscience E2:861–881.

Argaez, V., I. Solano-Zavaleta, and J.J. Zúñiga-Vega. 2018. Another potential cost of tail

 autotomy: tail loss may result in high ectoparasite loads in *Sceloporus* lizards.

 Amphibia-Reptilia 39:191–202.

Ashton, K. 2001. Body size variation among mainland populations of the western

 rattlesnake (*Crotalus viridis*). Evolution 55:2523–2533.

Berns, C.M. 2013. The evolution of sexual dimorphism: understanding mechanisms of

 sexual shape differences. Pp. 1–16 *In* Sexual Dimorphism. 1st Edition. Moriyama, H.

 (Ed.), InTech, Croatia.

Bock, B.C., A.M. Zapata, and V.P. Paez. 2010. Survivorship rates of adult *Anolis*

 mariarum (Squamata: Polychrotidae) in two populations with differing mean and

 asymptotic body sizes. Papeis Avulsos de Zoologica 50:43–50.

Buckley, L.B., G.H. Rodda, and W. Jetz. 2008. Thermal and energetic constraints on

 ectotherm abundance: a global test using lizards. Ecology 89:48–55.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a

 practical information-theoretic approach. Springer-Verlag, New York, New York,

 USA.

Calsbeek, R., and B. Sinervo. 2002. Uncoupling direct and indirect components of female

 choice in the wild. Proceedings of the National Academy of Sciences 99:14897–

 14902.

Chamaillé-Jammes, S., M. Massot, P. Aragon, and J. Clobert. 2006. Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. Global Change Biology12:392–402.

Cooper Jr., W.E., and L.J. Vitt. 2002. Increased predation risk while mate guarding as a cost of reproduction for male broad-headed skinks (*Eumeces laticeps*). Acta Ethologica 5:19–23.

Dickman, C.R., M. Letnic, and P.S. Mahon. 1999. Population dynamics of two species of dragon lizards in arid Australia: the effects of rainfall. Oecologia 119:357–366.

Doughty, P., B. Sinervo, and G.M. Burghardt. 1994. Sex-biased dispersal in a polygynous lizard, *Uta stansburiana*. Animal Behaviour 47:227–229.

Duellman, W.E. 1961. The amphibians and reptiles of Michoacán, México. University of Kansas Publications, Museum of Natural History 15:1–148.

Ekner, A., Z. Sajkowska, K. Dudek, and P. Tryjanowski. 2011. Medical cautery units as a permanent and non-invasive method of marking lizards. Acta Herpetologica 6:229–236.

Endriss, D.A., E.C. Hellgren, S.F. Fox, and R.W. Moody. 2007. Demography of an urban population of the Texas Horned Lizard (*Phrynosoma cornutum*) in Central Oklahoma. Herpetologica 63:320–331.

Feria-Ortiz, M., A. Nieto-Montes de Oca, and I.H. Salgado U. 2001. Diet and reproductive biology of the viviparous lizard *Sceloporus torquatus torquatus* (Squamata: Phrynosomatidae). Journal of Herpetology 35:104–112.

Flesch, A.D., P.C. Rosen, and P. Holm. 2017. Long-term changes in abundances of Sonoran Desert lizards reveal complex responses to climatic variation. Global Change Biology 23:5492–5508.

Flores-Villela, O., and L. Canseco-Márquez. 2007. Riqueza de la Herpetofauna. Pp. 407–420 *In* Biodiversidad de la Faja Volcánica Transmexicana. Vega I.L., J.J. Morrone, and D. Espinosa-Organista (Eds). Comisión Nacional para el Conocimineto y Uso de la Biodiversidad–Universidad Nacional Autónoma de México, . México.

Franklin, A.B. 2001. Exploring ecological relationships in survival and estimating rates of population change using program Mark. Pp 350–356 *In*: Wildlife, land and people: priorities for the 21st century. Field, R., R.J. Warren, H. Okarma, and P.R. Sievert (Eds). Wildlife Society, Bethesda, Maryland, USA.

Godínez-Cano, E. 1985. Ciclo reproductivo de *Sceloporus megalepidurus megalepidurus* Smith (Reptilia: Sauria: Iguanidae), en la parte oriental de Tlaxcala, México. Dissertation. Universidad Nacional Autónoma de México, México 73 p.

Gómez-Mendoza, J. 2007. Contribución al conocimiento de la herpetofauna del municipio de Tepeji del Río de Ocampo, Hidalgo. Dissertation, Escuela Nacional de Estudios Profesionales Iztacala, Universidad Nacional Autónoma de México, Estado de México, México 64 p.

González-Ruiz, A. 1991. Aspectos de la ecología poblacional de *Sceloporus megalepidurus megalepidurus* Smith (Reptilia: Sauria: Iguanidae) en el oriente de Tlaxcala, México. Dissertation, Escuela Nacional de Estudios Profesionales Iztacala, Universidad Nacional Autónoma de México, México, México. 192 p.

Grosbois, V., O. Gimenez, J.M. Gaillard, R. Pradel, C. Barbraud, J. Clobert, A.P. Møller, and H.Weimerskirch. 2008. Assessing the impact of climate variation on survival in vertebrate populations. Biological Reviews 83:357–399.

Guillette, L.J., and G. Casas-Andreu. 1980. Fall reproductive activity in the high altitude Mexican lizard, *Sceloporus grammicus microlepidotus*. Journal of Herpetology 14:143–147.

Havemann, C.P., T.A. Retief, C.A. Tosh, and P.J.N. de Bruyn. 2016. Roan antelope *Hippotragus equinus* in Africa: a review of abundance, threats and ecology. Mammal Review 46:144–158.

Hernández-Márquez, A.E. 2016. Ecología térmica y uso de hábitat de una población de *Sceloporus megalepidurus* (Squamata: Phrynosomatidae) que ocurre en los alrededores de la laguna de Atexcac, Puebla. Dissertation, Facultad de Estudios Superiores Zaragoza, Universidad Nacional Autónoma de México, México, México. 53 p.

Huey, R.B., C.A. Deutsch, J.J. Tewksbury, L.J. Vitt, P.E. Hertz, H.J. Álvarez P., and T. Garland Jr. 2009. Why tropical forest lizards are vulnerable to climate warming. Proceedings of the Royal Society B: Biological Sciences 276:1939–1948.

Instituto Nacional de Estadística y Geografía (INEGI). 2002. Cuaderno Estadístico Municipal: Nopala de Villagrán. Aguascalientes City: INEGI.

Jiménez-Cruz, E., A. Ramírez-Bautista, J.C. Marshall, M. Lizana-Avia, and A. Nieto-Montes de Oca. 2005. Reproductive cycle of *Sceloporus grammicus* (Squamata: Phrynosomatidae) from Teotihuacán, México. The Southwest Naturalist 50:178–187.

Jones, S.M., and R.E. Ballinger. 1987. Comparative life histories of *Holbrookia maculata* and *Sceloporus undulatus* in western Nebraska. Ecology 68:1828–1838

Katz, E.M., K.A. Tolley, and R. Altwegg. 2013. Survival and abundance of cape dwarf chameleons, *Bradypodion pumilum*, inhabiting a transformed, semi-urban wetland. Herpetological Journal 23:179–186.

Kearney, R. M. 2013. Activity restriction and the mechanistic basis for extinctions under climate warming. Ecology Letters 16:1470–1479.

Kearney, M., and W.P. Porter. 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. Ecology 85:3119–3131.

Kendall, W.L., K.H. Pollock, and C. Brownie. 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. Biometrics 51:293–308.

Kendall, W.L., J.D. Nichols, and J.E. Hines. 1997. Estimating temporary emigration using capture recapture data with Pollock's robust design. Ecology78:563–578.

Kendall, W.L. 1999. Robustness of closed capture–recapture methods to violations of the closure assumption. Ecology 80:2517–2525.

LaManna, J.A., T.L. George, J.F. Saracco, M.P. Nott, and D.F. DeSante. 2012. El Niño-Southern oscillation influences annual survival of a migratory songbird at a regional scale. The Auk 129:734–743.

Le Galliard, J.F., O. Marquis, and M. Massot. 2010. Cohort variation, climate effects, and population dynamics in a short-lived lizard. Journal of Animal Ecology 79:1296–1307.

Levy, O., L.B. Buckley, T.H. Keitt, C.D. Smith, K.O. Boateng, D.S. Kumar, and M.J. Angilletta Jr. 2015. Resolving the life cycle alters expected impacts of climate change. Proceedings of the Royal Society B 282:1–9.

Leyte-Manrique, A., and A. Ramírez-Bautista. 2010. Diet of two population of *Sceloporus grammicus* (Squamata: Phrynosomatidae) from Hidalgo, Mexico. The Southwestern Naturalist 55:98–103.

Martínez-Méndez, N., and F.R. Méndez-de la Cruz. 2007. Molecular phylogeny of the *Sceloporus torquatus* species-group (Squamata: Phrynosomatidae). Zootaxa 1609:53–68.

Mayhew, W.W. 1963. Reproduction in the granite spiny lizard, *Sceloporus orcutti*. Copeia 1963:144–152.

McCoy, E D., P.P. Hartmann, and H.R. Mushinski. 2004. Population biology of the rare Florida scrub lizard in fragmented habitat. Herpetologica 60:54–61.

McKay, J.L., and B.L. Phillips. 2012. Climatic determinants of the reproductive timing in the Asian house gecko, *Hemidactylus frenatus* Duméril and Bibron (Gekkonidae). The Raffles Bulletin of Zoology 60:583–588.

Niewiarowski, P.H., M.J. Angilletta Jr, and A.D. Leaché. 2004. Phylogenetic comparative analysis of life-history variation among populations of the lizard *Sceloporus undulatus*: an example and prognosis. Evolution 58:619–633.

Oro, D., R. Torres, C. Rodríguez, and H. Drummond. 2010. Climatic influence on demographic parameters of a tropical seabird varies with age, and sex. Ecology 91:1205–1214.

Ortega, A., and R. Barbault. 1984. Reproductive cycles in the mesquite lizard *Sceloporus grammicus*. Journal of Herpetology 18:168–175.

Ortega-León, A.M., E.R. Smith, J.J. Zúñiga-Vega, and F.R. Méndez-de la Cruz. 2007. Growth and demography of one population of the lizard *Sceloporus mucronatus mucronatus*. Western North American Naturalist 67:492–502.

Ortega-Rubio, A., G. Halffter, and R. Barbault. 2000. Bunch grass lizard, *Sceloporus scalaris*, population dynamics at La Michilia Biosphere Reserve, Mexico. Herpetological Journal 10:33–39.

Owen-Smith, N., D.R. Mason, and J.O. Ogutu. 2005. Correlates of survival rates for 10 African ungulate populations: density, rainfall, and predation. Journal of Animal Ecology 74:774–788.

Pastro, L.A., C.R. Dickman, and M. Letnic. 2013. Effects of wildfire, rainfall, and region on desert lizard assemblages: the importance of multi-scale processes. Oecologia 173:603–614.

Paxton, K.L, E.B. Cohen, E.H. Paxton, Z. Németh, and F.R. Moore. 2014. El Niño-Southern oscillation is linked to decreased energetic condition in long-distance migrants. PLoS ONE 9e95383.

Pérez-Mendoza, H.A., and J.J. Zúñiga-Vega. 2014. A test of the fast-slow continuum model of life-history variation in the lizard *Sceloporus grammicus.* Evolutionary Ecology Research 16:235–248.

Pérez-Mendoza, H.A., J.J. Zúñiga-Vega, C. Martorell, Y.H. Zurita-Gutiérrez, I. Solano-Zavaleta, A.L. Hernández-Rosas, and A. Molina-Moctezuma. 2014. Patterns of spatio-temporal variation in the survival rates of a viviparous lizard: the interacting effects of sex, reproductive trade-offs, aridity, and human-induced disturbance. Population Ecology 56:605–618.

Pollock, K.H., J.D. Nichols, C. Brownie, and J.E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107:3–97.

Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics 52:703–709.

Ramírez-Bautista, A., and A. González-Romero. 2002. Some reproductive and feeding

    characteristics of the viviparous Mexican lizard *Sceloporus torquatus*

    (Phrynosomatidae). The Southwestern Naturalist 47:98–102.

Ramírez-Bautista, A., E. Jiménez-Cruz, and J. Marshall. 2004. Comparative life history for

    populations of the *Sceloporus grammicus* complex (Squamata: Phrynosomatidae).

    Western North American Naturalist 64:175–183.

Ramírez-Bautista, A., A.L. Ortiz-Cruz, M.C. Arizmendi, and J. Campos. 2005.

    Reproductive characteristics of two syntopic lizard species, *Sceloporus gadoviae* and

    Sceloporus jalapae (Squamata: Phrynosomatidae) from Tehuacán Valley, Puebla,

    México. Western North American Naturalist 65:202–209.

Ramírez-Bautista, A., U. Hernández-Salinas, U.O. García-Vázquez, A. Leyte-Manrique,

    and L. Canseco-Márquez. 2009. Herpetofauna del Valle de México: diversidad y

    conservación. 1st Edition. Universidad Autónoma del Estado de Hidalgo, México.

    213 p.

Ramírez-Bautista, A., B.P. Stephenson, A. Lozano, H. Uribe-Rodríguez, and A. Leyte M.

    2012. Atypical reproductive cycles in population of *Sceloporus grammicus*

    (Squamata: Phrynosomatidae) from the Mexican Plateau. Ecology and Evolution

    2:1903–1913.

Ramírez-Bautista, A., U. Hernández-Salinas, and J.G. Zamora-Abrego. 2016. Growth

    ecology of the tree lizard *Urosaurus bicarinatus* (Squamata: Phrynosomatidae), in a

    tropical dry forest of the Chamela Region, Mexico. Animal Biology 66:189–199.

Read, J.L., K.J. Kovac, B.W. Brook, and D.A. Fordham. 2012. Booming during a bust: asynchronous population responses of arid zone lizards to climatic variables. Acta Oecologia 40:51–61.

Rojo, A., and J. Rodríguez. 2002. La flora del Pedregal de San Ángel. Instituto Nacional de Ecología. México.

Roth-Monzón, A.J., A.A. Mendoza-Hernández, O.A. Flores-Villela. 2018. Amphibian and reptile biodiversity in the semi-arid of the municipality of Nopala de Villagrán, Hidalgo, México. PeerJ 6:e4202.

Rzedowski, J. 2006. Vegetación de México. 1st Digital Edition. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO). México. 504 p.

Sánchez-Herrera, O. 1980. Diagnosis preliminar de la herpetofauna de Tlaxcala, México. Dissertation, Facultad de Ciencias, Universidad Nacional Autónoma de México, México. 155 p.

Sandvik, H., K. Erikstad, and B.E. Sæther. 2012. Climate affects seabird population dynamics both via reproduction, and adult survival. Marine Ecology Progress Series 454:273–284.

SEREPSA (Secretaría Ejecutiva de la Reserva Ecológica Pedregal de San Ángel). 2013. Portal oficial de la Reserva Ecológica Pedregal de San Ángel. Coordinación de la Investigación Científica, UNAM. Ciudad Universitaria, México, D.F. Fecha de creación: 4-sep-2013. URL: http://www.repsa.unam.mx.

Sillett, T.S., R.T. Holmes, and T.W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288:2040–2042.

Sinervo, B., F. Méndez-de la Cruz, D.B. Miles, B. Heulin, E. Bastiannans, M.V Cruz. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328:894–899.

Smith, A., C. Bull, D. Driscoll. 2012. Post-fire succession affects abundance and survival but not detectability in a knob-tailed gecko. Biological Conservation 145:139–147.

Smith, H.M. 1936. Description of new species of lizards of the genus *Sceloporus* from Mexico. Proceedings of the Biological Society of Washington 49:87–96.

Smith, H.M. 1939.The Mexican and Central American lizards of the genus *Sceloporus*. Field Museum of Natural History, Publications in Zoology Series 26:1–397.

Smith, G.R., and J.A Lemos-Espinal. 2005. Comparative escape behavior of four species of Mexican phrynosomatid lizards. Herpetologica 61:225–232.

Sites, J.W. Jr., J.W. Archie, C.J. Cole, and O. Flores-Villela. 1992. A review of phylogenetic hypotheses for lizards of the genus *Sceloporus* (Phrynosomatidae): implications for ecological and evolutionary studies. Bulletin of the American Museum of Natural History 213:1–110.

Ujvari, B., P. Fisher, J. Rydell, R. Wahlgren, B. Wright, and T. Madsen. 2015. Population demography of frillneck lizards (*Chlamydosaurus kingii*, Gray 1825) in the wet-dry tropics of Australia. Austral Ecology 40:60–66.

Wang, G., N.T. Hobbs, S. Twombly, R.B. Boone, A.W. Illius, I.J. Gordon, and J.E. Gross. 2009. Density dependence in northern ungulates: interactions with predation and resources. Population Ecology 51:123–132.

Weiss, S.L. 2001. The effect of reproduction on food intake of a sit-and-wait foraging lizard, *Sceloporus virgatus*. Herpetologica 57:138–146.

White, G.C., and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Suppl):120–138.

Wolf, A.J., E.C. Hellgren, E.M. Schauber, V. Bogosian, R.T. Kazmaier, D.C. Ruthven, and R.W. Moody. 2014. Variation in vital-rate sensitivity between populations of Texas horned lizards. Population Ecology 56:619–631.

Wright L.J., R.A. Hoblyn, R.E. Green, C.G. Bowden, J.W. Mallord, W.J. Sutherland, and P.M. Dolman. 2009. Importance of climatic, and environmental change in the demography of a multi-brooded passerine, the woodlark *Lullula arborea*. Journal of Animal Ecology 78:1191–1202.

Zúñiga-Vega, J.J. 2011. Estimating potential reproductive costs in the survival of a xenosaurid lizard. Herpetological Journal 21:117–129.

TABLE 1. Best-fitting Pradel models that examine variation in rates of survival (φ),

recapture (p), and recruitment (f) of three lizard species of the genus *Sceloporus*. The fit of

each model was evaluated using the Akaike information criterion adjusted for small sample

sizes (AICc). ΔAICc indicates the difference in the AICc value of each model with respect

to the top model. We only show models with ΔAICc < 2. Akaike weights (w) indicate the

relative support for each model in the data. The demographic rates may vary as a function

of sex (s), season (e), the additive effect of sex and season ($s + e$), and the interaction

between sex and season ($s \times e$). We also considered intercept-only (null) models (.). In

addition, for recapture probability (p), we evaluated the effects of temperature ($temp$), the

additive effect of temperature and sex ($temp + s$) and the interaction between temperature

and sex ($temp \times s$).

Species	Model	AICc	ΔAICc	w
Sceloporus torquatus	$\varphi\,(s + e)\,p\,(s \times e)\,f\,(s \times e)$	3424.22	0	0.34
	$\varphi\,(s \times e)\,p\,(s \times e)\,f\,(s \times e)$	3425.26	1.05	0.20
	$\varphi\,(e)\,p\,(s \times e)\,f\,(e)$	3425.83	1.61	0.15
Sceloporus grammicus	$\varphi\,(s + e)\,p\,(s \times e)\,f\,(s \times e)$	4413.69	0	0.28
	$\varphi\,(s \times e)\,p\,(s \times e)\,f\,(s + e)$	4414.68	1	0.17
	$\varphi\,(s \times e)\,p\,(s \times e)\,f\,(e)$	4415.55	1.87	0.11

Sceloporus

megalepidurus	φ *(e) p (.) f (s + e)*	3834.09	0	0.08
	φ *(e) p (temp) f (s + e)*	3834.13	0.04	0.08
	φ *(.) p (e) f (s + e)*	3834.15	0.06	0.08
	φ *(e) p (temp) f (s × e)*	3834.41	0.32	0.07
	φ *(e) p (s) f (s + e)*	3834.97	0.88	0.05
	φ *(s + e) p (temp) f (s + e)*	3835.19	1.10	0.05
	φ *(.) p (s + e) f (s + e)*	3835.20	1.11	0.05
	φ *(.) p (e) f (s × e)*	3836.02	1.94	0.03

TABLE 2. Best-fitting robust design models that examine variation in rates of survival (φ), recapture (p), and temporary emigration (γ) of three lizard species of the genus *Sceloporus*. The fit of each model was evaluated using the Akaike information criterion adjusted for small sample sizes (AICc). ΔAICc indicates the difference in the AICc value of each model with respect to the top model. We only show models with ΔAICc < 2. Akaike weights (w) indicate the relative support for each model in the data. The demographic rates may vary as a function of sex (s), season (e), the additive effect of sex and season ($s + e$), and the interaction between sex and season ($s \times e$). We also considered intercept-only (null) models (.). In addition, for recapture probability (p), we evaluated the effects of daily temperature (*temp*), the additive effect of daily temperature and sex (*temp + s*) and the interaction between daily temperature and sex (*temp $\times$ s*).

Species	Model	AICc	Δ AICc	w
Sceloporus torquatus	φ ($s + e$) γ (.) p ($s \times e$)	5250.78	0	0.52
	φ ($s + e$) γ (s) p ($s \times e$)	5250.97	0.19	0.47
Sceloporus grammicus	φ ($s \times e$) γ (.) p (*temp $\times$ s*)	6533.26	0	0.23
	φ ($s \times e$) γ (.) p (*temp*)	6533.36	0.1	0.22
	φ ($s \times e$) γ (.) p (*temp + s*)	6535.06	1.80	0.09

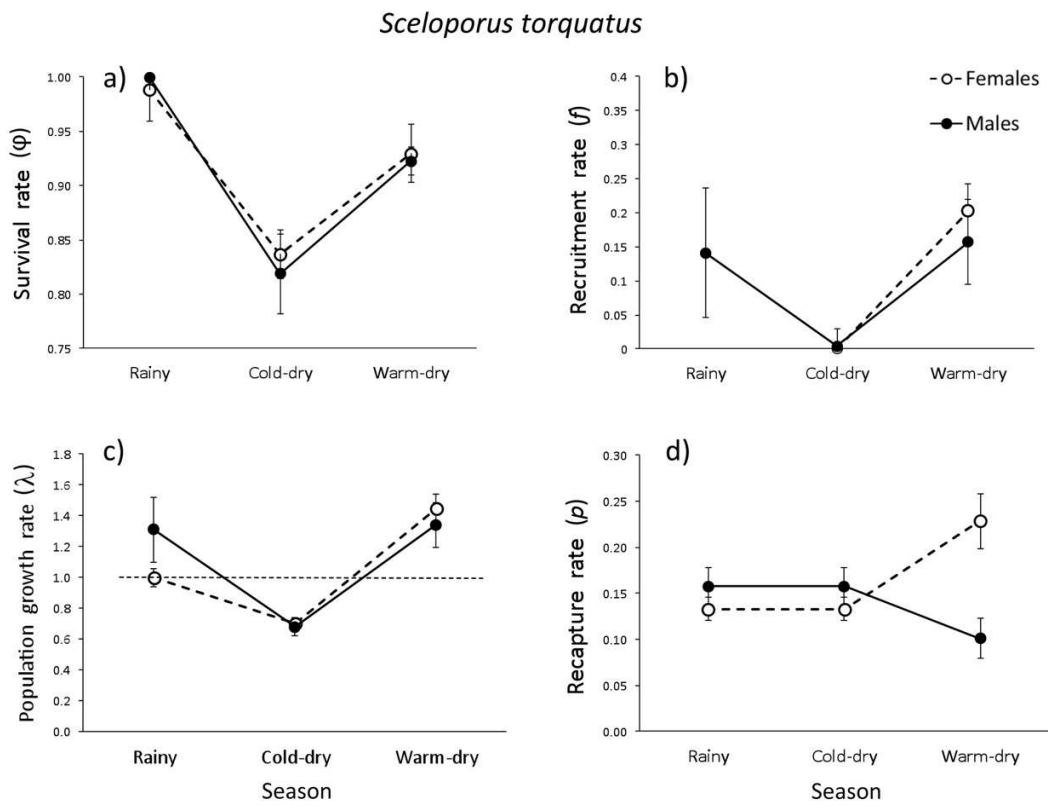|				
Sceloporus				
megalepidurus	φ *(s × e)* γ *(.) p (temp × s)*	5096.81	0	0.15
	φ *(e)* γ *(.) p (temp × s)*	5097.36	0.55	0.11
	φ *(.)* γ *(.) p (temp × s)*	5097.68	0.87	0.09
	φ *(s × e)* γ *(s) p (temp × s)*	5098.66	1.85	0.06

FIGURE 1. Model-averaged estimates of survival (a), recruitment (b), population growth (c), and recapture rates (d) for males and females of *Sceloporus torquatus.* Error bars indicate one standard error.
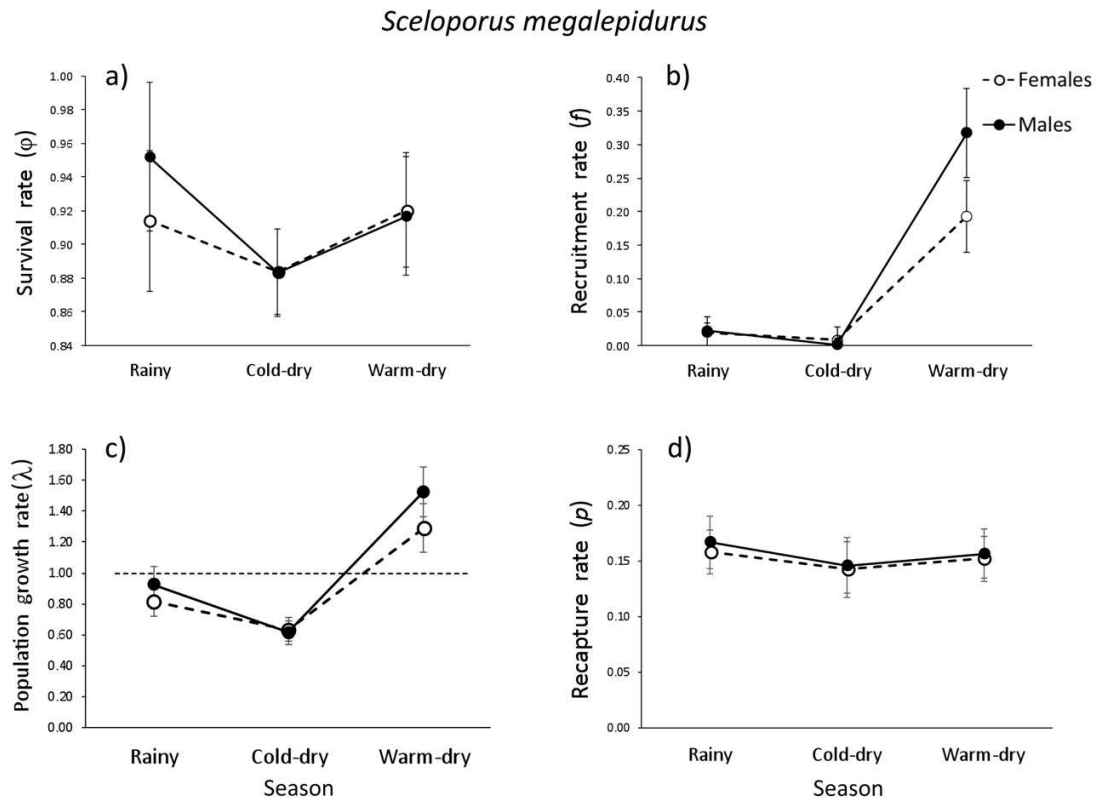

Sceloporus torquatus

FIGURE 2. Model-averaged estimates of survival (a), recruitment (b), population growth

(c), and recapture rates (d) for males and females of *Sceloporus grammicus*. Error bars

indicate one standard error.
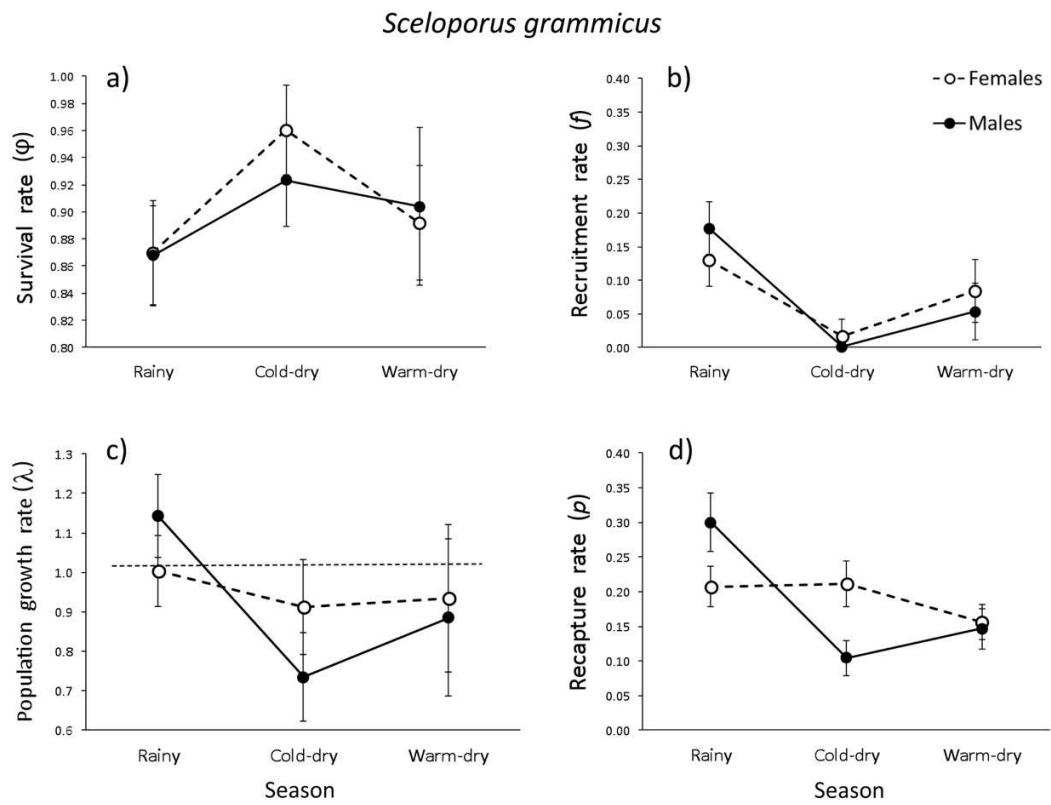
FIGURE 3. Model-averaged estimates of survival (a), recruitment (b), population growth (c), and recapture rates (d) for males and females of *Sceloporus megalepidurus.* Error bars indicate one standard error.

Sceloporus megalepidurus

FIGURE 4. Model-averaged estimates of temporary emigration (a) and population abundance (b) for males and females of *Sceloporus torquatus.* Error bars indicate one standard error.
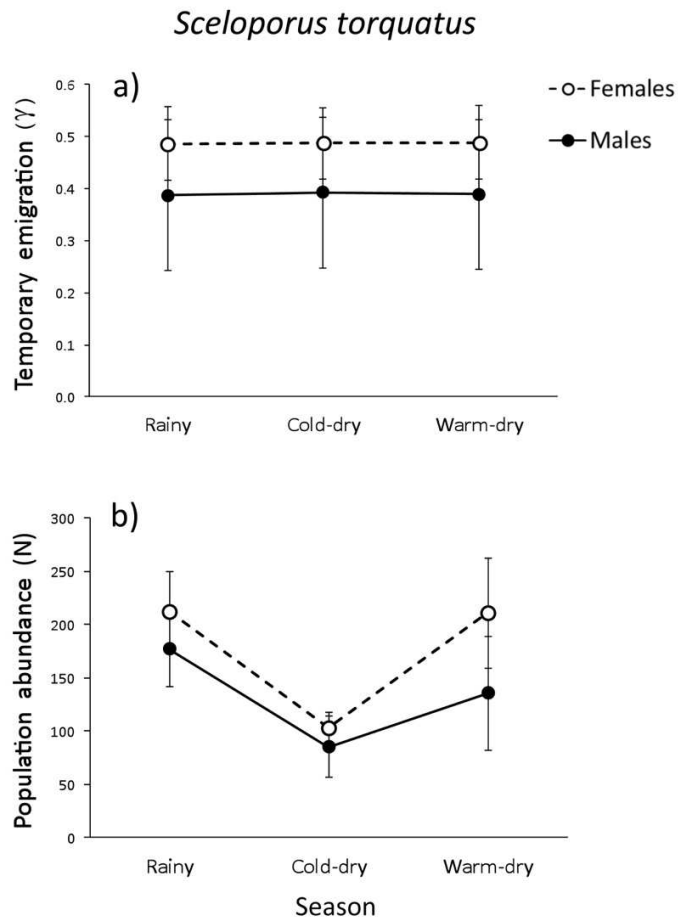
FIGURE 5. Model-averaged estimates of temporary emigration (a) and population abundance (b) for males and females of *Sceloporus grammicus*. We also show the estimated effects of daily temperature on recapture rates (c). Error bars indicate one standard error.
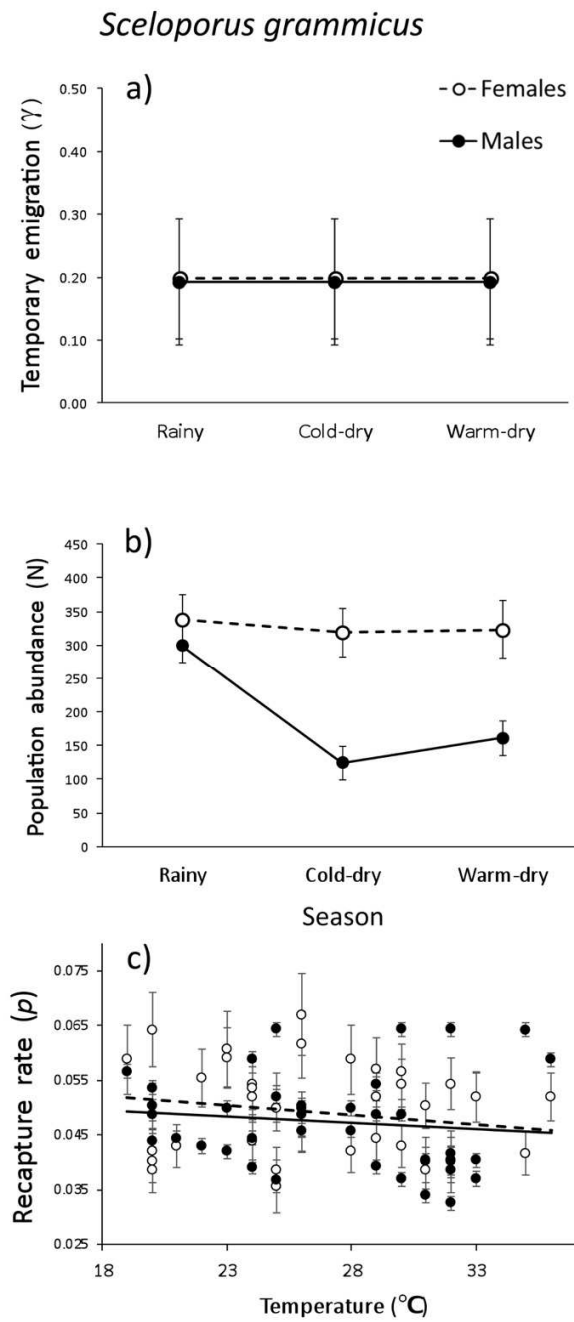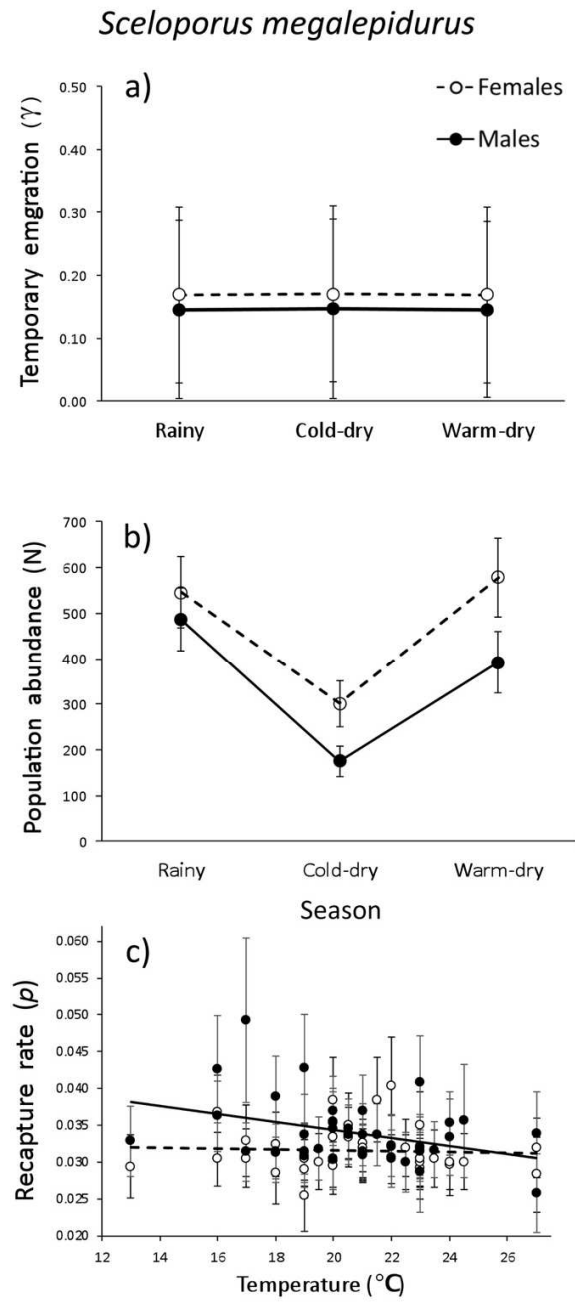
FIGURE 6. Model-averaged estimates of temporary emigration (a) and population abundance (b) for males and females of *Sceloporus megalepidurus.* We also show the estimated effects of daily temperature on recapture rates (c). Error bars indicate one standard error.

DISCUSIÓN

Los resultados de esta investigación revelan cambios sustanciales en las tasas vitales a lo largo de un ciclo anual en las tres especies de lagartijas. Sin embargo, hubo claras diferencias entre especies, lo que indica que cada una de ellas experimenta diferentes procesos ecológicos que a su vez promueven distintos patrones de variación estacional en los parámetros demográficos. Toda esta información representa una contribución importante al conocimiento demográfico de especies del género *Sceloporus* y, en general, sugiere que otros reptiles también experimentan cambios drásticos entre temporadas en sus tasas vitales.

En organismos ectotérmicos, la temperatura juega un papel clave en los procesos fisiológicos (Woolrich-Piña et al., 2006; Abram et al. 2017). En lagartijas, los procesos como la digestión, la resistencia a enfermedades, la gestación y el periodo de actividad y su relación con la temperatura están bien documentados (Angilletta et al. 2002; Kearney et al. 2004; Le Galliard et al. 2010; McKay y Phillips 2012). Durante la temporada seca y fría la supervivencia de ambos sexos de *S. torquatus* fue más baja en comparación con las temporadas de lluvias y seca y cálida. Esto podría deberse a que el aumento en las restricciones térmicas puede tener como consecuencia una mayor mortalidad debido a la disminución de funciones vitales como el metabolismo y el sistema inmune (Angilletta et al. 2004, 2010; Chamaillé-Jammes et al. 2006).

En especies de mayor tamaño como *S. torquatus* la ganancia de calor para la termorregulación es mucho más lenta, es decir, el tiempo que tardan en alcanzar temperaturas óptimas es mayor (Hailey 1982; Carothers et al. 1997). Esto podría aumentar su actividad de termorregulación, lo que a su vez provoca un costo en términos de supervivencia (Adolph y Porter 1993). Para poner a prueba esta hipótesis es necesario

llevar a cabo observaciones detalladas de actividad a lo largo del año y, sobre todo, comparar estas observaciones entre las tres especies de lagartijas, puesto que la mayor mortalidad en la temporada seca y fría sólo se observó en *S. torquatus* y no en las otras dos especies.

Por el contrario, en *S. grammicus* presentó para las hembras una tasa de supervivencia ligeramente mayor en la temporada seca y fría, mientras que en *S. megalepidurus* no encontramos diferencias entre estaciones. La disponibilidad de sitios que reciben directamente la luz solar y que sirven de sitios de percha para las lagartijas es menor en los microhábitats de *S. torquatus* en comparación con *S. grammicus* y *S. megalepidurus*. Una mayor cobertura de árboles implica menor cantidad de sitios que reciben luz solar directa. En contraste, nuestras poblaciones de *S. grammicus* y *S. megalepidurus* se encuentran en matorrales xerófilos con vegetación mucho más abierta y de menor altura lo que permite un mejor flujo de aire, factor importante para organismos ectotérmicos que pierden calor por convección (Hernández 2016). Por lo tanto, nuestros resultados nos permiten proponer la hipótesis de que la calidad térmica de los microhábitats es mejor para estas últimas dos especies.

El aumento de la supervivencia de las hembras de *S. grammicus* en la época seca y fría podría asociarse a un efecto conductual con respecto a las otras dos especies. Si bien las hembras de las tres especies están gestantes durante el invierno (Ramírez-Bautista y González-Romero 2002; Jiménez-Cruz et al. 2005; González-Ruiz 1991) y durante la gestación diversas especies de lagartijas experimentan menor movilidad y forrajean con menor frecuencia (Weiss 2001; Sinervo et al. 2010), las hembras de *S. grammicus* podrían ser las que tengan las tasas más bajas de actividad en comparación con las otras dos

especies, lo que las hace notablemente menos conspicuas a los depredadores. Además de que, al ser más pequeña que *S. torquatus*, el alcanzar temperaturas óptimas en un tiempo más corto el tiempo que deben arriesgarse ante depredadores podría disminuir. Además, debido a que *S. torquatus* es de mayor tamaño, probablemente las hembras gestantes tienen una mayor vulnerabilidad porque son más pesadas y, en consecuencia, tienen menor movilidad (Bauwens 1981).

Únicamente en *S. grammicus* encontramos una relación entre la tasa de reclutamiento de ambos sexos y la época reproductiva, donde el reclutamiento aumentó en la época de lluvias. En contraste, la tasa de reclutamiento de adultos de *S. megalepidurus* fue notablemente baja tanto en lluvias como en secas frías. En la temporada de secas cálidas, aproximadamente seis meses antes de los apareamientos, el reclutamiento de esta última especie aumentó tanto para hembras como para machos. De esta manera se respaldan los hallazgos de Hernández (2016) donde encontró que esta especie no es territorial. Es decir, el incremento en el reclutamiento de adultos no está asociado a la defensa de territorios, sino que podría ser resultado de un mayor movimiento de los individuos hacia lugares con una mayor disponibilidad de alimento en la época más seca y caliente del año, durante la cual la abundancia de presas potenciales (i.e., invertebrados) es notablemente baja (Ramírez-Bautista et al. 2016). Tampoco encontramos apoyo para esta hipótesis en *S. torquatus*. El reclutamiento de adultos de esta especie fue relativamente alto tanto en lluvias como en secas cálidas. Por lo tanto, presumiblemente este proceso no está estrictamente asociado a la temporada previa a los apareamientos. Este resultado podría estar relacionado con el hecho de que durante la temporada de secas cálidas y la de lluvias

el aumento de la temperatura o de la disponibilidad de alimento (respectivamente) haya incrementado los patrones de actividad y de movimiento de los individuos.

La tasa de emigración temporal está asociada con el movimiento de los individuos a través del espacio (Kendall y Nichols 1995; Kendall et al. 1997). Desafortunadamente sólo pudimos poner a prueba esta hipótesis con los datos de *S. torquatus* (con las otras dos especies tuvimos problemas de convergencia de los modelos al incorporar la estacionalidad en la tasa de emigración temporal) y no encontramos evidencia de variación entre estaciones ni entre sexos. Sin embargo, debemos destacar que en cada mes, entre el 40% y el 50% de los individuos marcados de *S. torquatus* se encontraban fuera del área de estudio. Esto representa evidencia de que estas lagartijas se desplazan a lo largo de distancias considerables durante todo el año, independientemente de la fase del ciclo reproductivo.

A grandes rasgos, la relación entre las variaciones estacionales y su efecto en las tasas de reclutamiento y supervivencia sobre la abundancia poblacional fueron congruentes. En *S. torquatus* durante la temporada de secas frías disminuyó la supervivencia y el reclutamiento de ambos sexos lo que genera una menor abundancia y tasa de crecimiento poblacional. En *S. grammicus*, la disminución de machos en la temporada de secas frías concuerda con el menor registro de la tasa de reclutamiento. Esto genera un patrón de proporción sexual sesgado hacia las hembras en *S. grammicus* durante las temporadas secas del año. Otros estudios con lagartijas también han encontrado que las hembras son más abundantes que los machos (Ortega-Rubio et al. 2000; Katz et al. 2013). Una proporción sexual sesgada puede tener serias consecuencias, puesto que puede afectar negativamente el éxito reproductivo total de los individuos de la población y, en el largo plazo, generar tendencias demográficas negativas. Por lo tanto, esta proporción sexual con sesgo hacia las

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hembras que observamos tanto en *S. grammicus* como en *S. megalepidurus* merece futura atención.

En *S. megalepidurus* tanto la abundancia como la tasa de crecimiento poblacional decrecieron durante la temporada seca y fría que corresponde con el menor registro del reclutamiento de adultos de ambos sexos. También en esta especie encontramos que hubo más hembras que machos en las temporadas secas. Esta proporción sexual sesgada hacia hembras puede disminuir la competencia entre machos por parejas potenciales (McCoy et al. 2004; Bock et al. 2010). Esto a su vez generaría machos relativamente más pequeños (Berns, 2013). De acuerdo con esta hipótesis, el dimorfismo sexual más marcado por talla sucede en *S. torquatus*, que es la especie en la que no encontramos diferencias en las abundancias entre sexos y en la que los machos son notablemente más grandes que las hembras (Ramírez-Bautista y González-Romero 2002). En *S. grammicus* existe dimorfismo sexual por talla pero moderado (Jiménez-Cruz et al. 2005) y en *S. megalepidurus* no hay dimorfismo sexual por talla (González-Ruiz 1991).

CONCLUSIÓN

El análisis de las tasas demográficas a una escala intra-anual nos permitió observar en qué temporadas del año ocurren cambios drásticos en la supervivencia, el reclutamiento y la abundancia de nuestras tres especies de estudio. Además, reportamos por primera vez para especies del género *Sceloporus* estimaciones de la tasa de emigración temporal hacia fuera de las áreas de estudio. En general, las hipótesis que propusimos sobre los factores potencialmente causales de la variación intra-anual en las tasas vitales sólo se cumplieron

parcialmente, puesto que los patrones de variación estacional en las tasas vitales y en la abundancia no fueron consistentes entre las tres especies. La supervivencia disminuye en la temporada seca y fría solamente en *S. torquatus*. El reclutamiento aumenta durante la estación de lluvias solamente en *S. grammicus*, probablemente debido a la incorporación de nuevos individuos reproductivos a la población antes de los apareamientos. Finalmente, con respecto a la emigración temporal (que sólo pudimos estimar para *S. torquatus*) no detectamos variación estacional, pero sí descubrimos que entre el 40% y el 50% de los individuos que marcamos y recapturamos se encontraban fuera del área de estudio en cada ocasión de muestreo, lo que nos indica que estas lagartijas pueden moverse a través de distancias relativamente largas durante todo el año. Las notables diferencias que encontramos entre estas tres especies de lagartijas del género *Sceloporus* en sus dinámicas poblacionales intra-anuales indican que los procesos ecológicos locales que operan en el corto plazo (a escala mensual o estacional) pueden ser dramáticamente distintos entre localidades relativamente cercanas y, además, que sus consecuencias en las tasas vitales de los seres vivos también pueden ser notablemente diferentes aún entre especies de un mismo género.

Literatura citada

Abram, P.K., G. Boivin, J. Moiroux, and J. Brodeur. 2017. Behavioral effects of temperature on ectothermic animals: unifying thermal physiology and behavioral plasticity. Biological Reviews 92:1859–1876.

Adolph, S. C., & Porter, W. P. (1993). Temperature, activity, and lizard life histories. The American Naturalist 142: 273-295.

Andrews, R. M. 1998. Geographic variation in the field body temperature of Sceloporus lizards. Journal of Thermal Biology. 23: 329-334.

Angilletta, Jr. M.J., B.S. Cooper, M.S. Schuler, and J.G. Boyles. 2010. The evolution of thermal physiology in endotherms. Frontiers in Bioscience E2:861–881.

Angilletta, Jr. M.J., P.H. Niewiarowski, A.E. Dunham, A.D. Leaché, and W.P. Porter. 2004. Bergmann's clines in ectotherms: illustrating a life-history perspective with sceloporine lizards. The American Naturalist 164:E168–E183.

Bailey, N.T.J. 1964. The elements of stochastics processes with applications ton the Natural Sciences. Wiley, New Yok, USA.

Barlett, M.S. 1960. Stochastic population models in ecology and epidemiology. Methuen and Wiley, London, UK, and New York, USA.

Bauwens D. y C. Thoen. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard Lacerta vivipara. Journal of Animal Ecology 50.

Berns, C.M. 2013. The evolution of sexual dimorphism: understanding mechanisms of sexual shape differences. Pp. 1–16 *In* Sexual Dimorphism. 1st Edition. Moriyama, H. (Ed.), InTech, Croatia.

Bock, B.C., A.M. Zapata, and V.P. Paez. 2010. Survivorship rates of adult *Anolis mariarum* (Squamata: Polychrotidae) in two populations with differing mean and asymptotic body sizes. Papeis Avulsos de Zoologica 50:43–50.

Calsbeek, R., and B. Sinervo. 2002. Uncoupling direct and indirect components of female choice in the wild. Proceedings of the National Academy of Sciences 99:14897–14902.

Carothers, J.H., S.F. Fox, P. A. Marquet, and F.M. Jaksic. 1997. Thermal characteristics of ten Andean lizards of the genus Liolaemus in central Chile. Revista Chilena de Historia Natural 297-309.

Chamaillé-Jammes, S., M. Massot, P. Aragon, and J. Clobert. 2006. Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. Global Change Biology12:392–402.

Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO).2011. La Biodiversidad en Puebla: Estudio de Estado. México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Gobierno del Estado de Puebla, Benemérita Universidad Autónoma de Puebla. 440 pp.

Cooper Jr., W.E., and L.J. Vitt. 2002. Increased predation risk while mate guarding as a cost of reproduction for male broad-headed skinks (*Eumeces laticeps*). Acta Ethologica 5:19–23.

Dickman, C.R., M. Letnic, and P.S. Mahon. 1999. Population dynamics of two species of dragon lizards in arid Australia: the effects of rainfall. Oecologia 119:357–366.

Dugger, K.M., J. Faaborg, W.J. Arendt, and, K.A. Hobson. 2014. Understanding survival and abundance of overwintering warblers: Does rainfall matter? The Condor 106:744-760.

Feria-Ortiz, M., A. Nieto-Montes de Oca, and I.H. Salgado U. 2001. Diet and reproductive biology of the viviparous lizard *Sceloporus torquatus torquatus* (Squamata: Phrynosomatidae). Journal of Herpetology 35:104–112.

Flesch, A.D., P.C. Rosen, and P. Holm. 2017. Long-term changes in abundances of Sonoran Desert lizards reveal complex responses to climatic variation. Global Change Biology 23:5492–5508.

Godínez-Cano, E. 1985. Ciclo reproductivo de *Sceloporus megalepidurus megalepidurus* Smith (Reptilia: Sauria: Iguanidae), en la parte oriental de Tlaxcala, México. Dissertation. Universidad Nacional Autónoma de México, México 73 p.

González-Ruiz, A. 1991. Aspectos de la ecología poblacional de *Sceloporus megalepidurus megalepidurus* Smith (Reptilia: Sauria: Iguanidae) en el oriente de Tlaxcala, México. Dissertation, Escuela Nacional de Estudios Profesionales Iztacala, Universidad Nacional Autónoma de México, México, México. 192 p.

Grosbois, V., O. Gimenez, J.M. Gaillard, R. Pradel, C. Barbraud, J. Clobert, A.P. Møller, and H.Weimerskirch. 2008. Assessing the impact of climate variation on survival in vertebrate populations. Biological Reviews 83:357–399.

Hailey, A. 1982. Choice of substrate and heating rate in Lacerta vivipara. British Journal of
    Herpetology 6:207-213

Hernández, M.A.E. 2016. Ecología térmica y uso de hábitat de una población de
    Sceloporus megalepidurus (Squamata: Phrynosomatidae) que ocurre en los
    alredededores de la laguna de Atexcac, Puebla. Dissertation. Universidad Nacional
    Autónoma de México, Facultad de Estudios Superiores Zaragoza. 53 pp.

INEGI. 2009a. Carta Topográfica, Carta de Climas, Escala 1:1 000 000.

Jiménez-Cruz, E., A. Ramírez-Bautista, J.C. Marshall, M. Lizana-Avia, and A. Nieto-
    Montes de Oca. 2005. Reproductive cycle of *Sceloporus grammicus* (Squamata:
    Phrynosomatidae) from Teotihuacán, México. The Southwest Naturalist 50:178–187.

Katz, E.M., K.A. Tolley, and R. Altwegg. 2013. Survival and abundance of cape dwarf
    chameleons, *Bradypodion pumilum*, inhabiting a transformed, semi-urban wetland.
    Herpetological Journal 23:179–186.

Kendall, W.L. and J.D. Nichols. 1995. On the use of secondary capture–recapture samples
    to estimate temporary emigration and breeding proportions. J. Appl. Stat. 22, 751–
    762.

Kendall, W.L., J.D. Nichols, and J.E. Hines. 1997. Estimating temporary emigration using
    capture–recapture data with Pollock's robust design. Ecology 78:563–578.

Kearney, M., and W.P. Porter. 2004. Mapping the fundamental niche: physiology, climate,
    and the distribution of a nocturnal lizard. Ecology 85:3119–3131.

Laché, A.D., and J.W. Sites Jr. 2010. Chromosome evolution and diversification in North
American spiny lizards (Genus *Sceloporus*). Cytogenetic and genome research 127:
166-181.

LaManna, J.A., T.L. George, J.F. Saracco, M.P. Nott, and D.F. DeSante. 2012. El Niño-
Southern oscillation influences annual survival of a migratory songbird at a regional
scale. The Auk 129:734–743.

Lebreton, J.D., J.D. Nichols, R.J. Barker, R. Pradel, and J.A. Spendelow. 2009. Modeling
individual animal histories with multistate capture–recapture models. Advances in
ecological research 41:87-173.

Le Galliard, J.F., O. Marquis, and M. Massot. 2010. Cohort variation, climate effects, and
population dynamics in a short-lived lizard. Journal of Animal Ecology 79:1296–
1307.

Levy, O., L.B. Buckley, T.H. Keitt, C.D. Smith, K.O. Boateng, D.S. Kumar, and M.J.
Angilletta Jr. 2015. Resolving the life cycle alters expected impacts of climate
change. Proceedings of the Royal Society B 282:1–9.

Loehr, V.J.T. 2010. Structure and dynamics of a Namaqualand Speckled tortoise
(*Homophus signatus signatus*) population over 5 years of rainfall variation.
Chelonian Conservation and Biology 9:223-230.

McCoy, E D., P.P. Hartmann, and H.R. Mushinski. 2004. Population biology of the rare
Florida scrub lizard in fragmented habitat. Herpetologica 60:54–61.

McKay, J.L., and B.L. Phillips. 2012. Climatic determinants of the reproductive timing in the Asian house gecko, *Hemidactylus frenatus* Duméril and Bibron (Gekkonidae). The Raffles Bulletin of Zoology 60:583–588.

Newell, T. D. 2017. Effects of the thermal stress on survivorship of brook trout (*Salvelinus fontinalis*) in Aridondak lakes. Dissertation. Cornell University. 90 pp.

Ortega-Rubio, A., G. Halffter, and R. Barbault. 2000. Bunch grass lizard, *Sceloporus scalaris*, population dynamics at La Michilia Biosphere Reserve, Mexico. Herpetological Journal 10:33–39.

Paxton, K.L, E.B. Cohen, E.H. Paxton, Z. Németh, and F.R. Moore. 2014. El Niño-Southern oscillation is linked to decreased energetic condition in long-distance migrants. PLoS ONE 9e95383.

Pollock, K.H., J.D. Nichols, C. Brownie, and J.E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107:3–97.

Pradel, R. 1996. Utilization of capture–mark–recapture for the study of recruitment and population growth rate. Biometrics 52:703–709.

Pulliam, R.H. 1988. Sources, sinks, and population regulation. Am. Nat. 132: 652-661.

Ramírez-Bautista, A., and A. González-Romero. 2002. Some reproductive and feeding characteristics of the viviparous Mexican lizard *Sceloporus torquatus* (Phrynosomatidae). The Southwestern Naturalist 47:98–102.

Ramírez-Bautista, A., B.P. Stephenson, A. Lozano, H. Uribe-Rodríguez, and A. Leyte M. 2012. Atypical reproductive cycles in population of *Sceloporus grammicus* (Squamata: Phrynosomatidae) from the Mexican Plateau. Ecology and Evolution 2:1903–1913.

Ramírez-Bautista, A., U. Hernández-Salinas, and J.G. Zamora-Abrego. 2016. Growth ecology of the tree lizard *Urosaurus bicarinatus* (Squamata: Phrynosomatidae), in a tropical dry forest of the Chamela Region, Mexico. Animal Biology 66:189–199.

Read, J.L., K.J. Kovac, B.W. Brook, and D.A. Fordham. 2012. Booming during a bust: asynchronous population responses of arid zone lizards to climatic variables. Acta Oecologia 40:51–61.

Richard, E., S.E. Simpson, S.A. Medill, and P.D. McLoughlin. 2014. Interacting effect of age, density, and weather on survival and current reproduction for a large mammal. Ecology and Evolution 4:3851-3860.

Rzedowski, J. 1954. Vegetación del Pedregal de San Ángel, Distrito Federal, México. An. Esc. Nac. Cienc. Biol. México 8:59-129.

Rzedowski, J. 2006. Vegetación de México [Vegetation of Mexico]. Mexico City, México: CONABIO.

Salvidio, S., and F. Oneto. 2008. Density regulation in the Mediterranean leaf-toed gecko *Euleptes europaea*. Ecological Research 23:051-1055.

Sinervo, B., F. Méndez-de la Cruz, D.B. Miles, B. Heulin, E. Bastiannans, M.V Cruz. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328:894–899.

Sites, J. W., Jr., J.W. Archie, Ch.J. Cole, and O. Flores-Villela. 1992. A review of phylogenetic hypotheses for lizards of the genus Sceloporus (Phrynosomatidae): Implications for ecological and evolutionary studies. Bulletin of the American Museum of Natural History 213:1–110.

Smith, A., C. Bull, D. Driscoll. 2012. Post-fire succession affects abundance and survival but not detectability in a knob-tailed gecko. Biological Conservation 145:139–147.

Smith, G.R., and J.A Lemos-Espinal. 2005. Comparative escape behavior of four species of Mexican phrynosomatid lizards. Herpetologica 61:225–232.

Smith, H.M. 1939.The Mexican and Central American lizards of the genus *Sceloporus*. Field Museum of Natural History, Publications in Zoology Series 26:1–397.

Ujvari, B., P. Fisher, J. Rydell, R. Wahlgren, B. Wright, and T. Madsen. 2015. Population demography of frillneck lizards (*Chlamydosaurus kingii*, Gray 1825) in the wet-dry tropics of Australia. Austral Ecology 40:60–66.

Wang, G., N.T. Hobbs, S. Twombly, R.B. Boone, A.W. Illius, I.J. Gordon, and J.E. Gross. 2009. Density dependence in northern ungulates: interactions with predation and resources. Population Ecology 51:123–132.

Weiss, S.L. 2001. The effect of reproduction on food intake of a sit-and-wait foraging lizard, *Sceloporus virgatus*. Herpetologica 57:138–146.

Wiens, J.J., and T.W. Reeder. 1997. Phylogeny of spiny lizards (Sceloporus) based on molecular and morphological evidence. Herpetological Monographs 11:1–101.

Wolf, A.J., E.C. Hellgren, E.M. Schauber, V. Bogosian, R.T. Kazmaier, D.C. Ruthven, and R.W. Moody. 2014. Variation in vital-rate sensitivity between populations of Texas horned lizards. Population Ecology 56:619–631.

Woolrich-Piña G., J.A. Lemos-Espinal, O. López, M.M.E. Calderón, E.J.E. González, S.L.Correa y A.F. Montoya. 2006. Ecología térmica de una población de la lagartija *Sceloporus grammicus* (Iguanidae: Phrynosomatidae) que ocurre en la zona centro-oriente de la ciudad de México. Acta zoológica mexicana, 22(2):137-150.

Wright L.J., R.A. Hoblyn, R.E. Green, C.G. Bowden, J.W. Mallord, W.J. Sutherland, and P.M. Dolman. 2009. Importance of climatic, and environmental change in the demography of a multi-brooded passerine, the woodlark *Lullula arborea*. Journal of Animal Ecology 78:1191–1202.

Zúñiga-Vega, J.J. 2011. Estimating potential reproductive costs in the survival of a xenosaurid lizard. Herpetological Journal 21:117–129.

ANEXO

Métodos de campo.— Visitamos cada área de estudio durante un año y medio aproximadamente. Cada visita consta de muestreos primarios y muestreos secundarios según la estructura de muestreo clásico de diseño robusto de Pollock (Fig. 1). Durante los muestreos primarios la población se encuentra abierta a cambios demográficos como son los nacimientos, muertes, migración e inmigración. Durante los muestreos secundarios, se asume que debido a la cercanía temporal de los muestreos (días continuos en este caso) la población se encuentra demográficamente cerrada, es decir, no hay nacimientos, muertes, inmigración y emigración (Pollock et al. 1990).
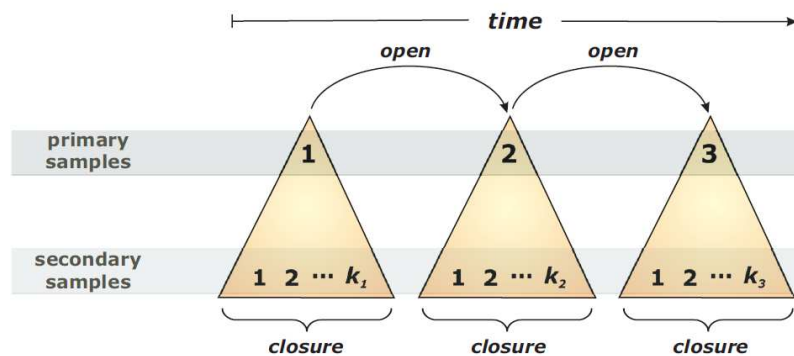
Figura 1. Estructura del modelo de muestreo clásico de diseño robusto de Pollock. Tomado de

Los intervalos de tiempo entre las ocasiones de muestreo primarias permiten la estimación de la supervivencia, la emigración temporal fuera del área de estudio, así como la inmigración de animales marcados al área de estudio. De la misma manera durante estos intervalos de muestreo se estima la probabilidad de captura y recaptura de cada individuo tomando en cuenta la detección imperfecta. Además de esto, podemos estimar la abundancia real durante nuestro muestreo como un parámetro derivado.

Los modelos Pradel nos permiten la estimación de la tasa de crecimiento poblacional realizada que es la tasa de crecimiento poblacional observada entre muestreos sucesivos (Pradel 1996). Los modelos Pradel permiten la estimación de la entrada a la población a través del reclutamiento (*f*). El reclutamiento se define como el número de individuos que entran a la población por cada individuo presente en la misma (Pradel 1996).

En cada muestreo realizamos el mismo recorrido como se establece en el modelo de diseño robusto de Pollock (Pollock et al. 1990). Durante las salidas a campo, se establecieron diez días consecutivos de trabajo, sin embargo, los datos de campo varían debido principalmente a condiciones climáticas desfavorables para las lagartijas. De esta manera, el número de días consecutivos de muestreo (muestreos secundarios) es diferente entre áreas de estudio y entre ocasiones de muestreo.

Áreas de estudio.— El jardín Botánico se encuentra en el núcleo suroriente dentro de la Reserva Ecológica del Pedregal de San Ángel al suroeste de la Ciudad de México (Fig.2). El clima es C(w1), es decir, subtipo templado subhúmedo (CONABIO 2011; INEGI 2009). El área de estudio presenta dos épocas secas, una de marcadas temperaturas frías durante el invierno y la otra de temperaturas cálidas (Fig. 3). Dentro del área de muestreo el tipo de vegetación es matorral xerófilo sobre un sustrato de roca volcánica que se encuentra dentro de la zona urbana (Rzedowski 1954).

Nopala de Villagrán se localiza al poniente del estado de Hidalgo (Fig. 2). El clima es C(w1), es decir, subtipo templado subhúmedo (CONABIO 2011; INEGI 2009). El tipo de vegetación es matorral xerófilo dentro de un área agrícola (Fig. 3).

La Laguna de Alchichica se localiza en la porción suroeste del municipio de

Tepeyahualco, Puebla (Fig. 2). El clima es BS1kw, es decir, subtipo semiseco templado

(CONABIO 2011; INEGI 2009). Presenta una estación seca y fría de diciembre a marzo y

una estación cálida y húmeda el resto del año (Alcocer et al. 2000). El tipo de vegetación es

matorral xerófilo (Fig. 3) donde los organismos más característicos pertenecen a los

géneros *Agave*, *Hechtia*, *Neolina* y *Dasylirion* (Rzedowski 2006). Las tres áreas de estudio

son relativamente similares ecológicamente ya que comparten el mismo tipo de vegetación

(matorral xerófilo), si bien no son idénticos, las especies presentes forman un estrato

arbustivo espinoso y perenifolio denso que proporcionan a las lagartijas sitios de percha y

refugios. En el caso particular del Jardín Botánico, *S. torquatus* es de hábitos saxícolas por

lo que utiliza las grietas formadas entre la roca volcánica como refugios (Feria-Ortíz et al.

2001).

El clima es templado subhúmedo tanto en el Jardín Botánico como en Nopala de

Villagrán. Para el análisis de datos se tomo en cuenta la estacionalidad establecida por

Feria-Ortiz y colaboradores (2001) como representativa del Valle de México donde

establecen que la temporada de lluvias ocurre principalmente de mayo a octubre y el

invierno es seco. Elaboramos un climograma con datos de temperatura ambiental y

precipitación anual del Jardín Botánico (Fig. 4), de Nopala de Villagrán (Fig. 5) y de la

laguna de Alchichica (Fig. 6) de las estaciones climatológicas más cercanas y de acuerdo

con esto se establecieron tres estaciones generales en el valle de México tomando en cuenta

los datos históricos. Existe un periodo de secas de septiembre a mayo, dentro de este

periodo las temperaturas más bajas se registran de noviembre a febrero, mientras que las

más calurosas se presentan durante marzo, abril y mayo. La temporada lluviosa ocurre entre
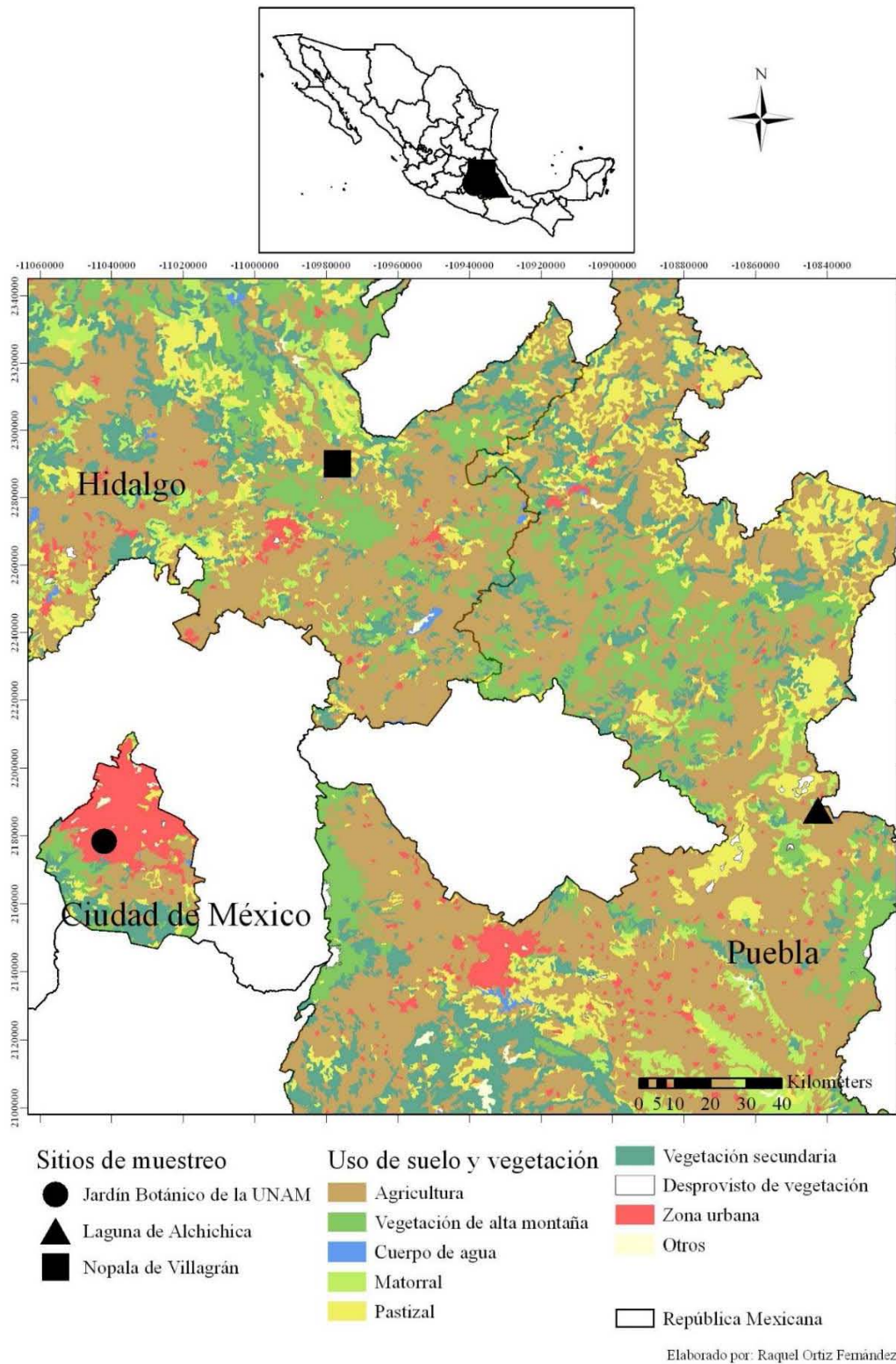
junio y agosto.

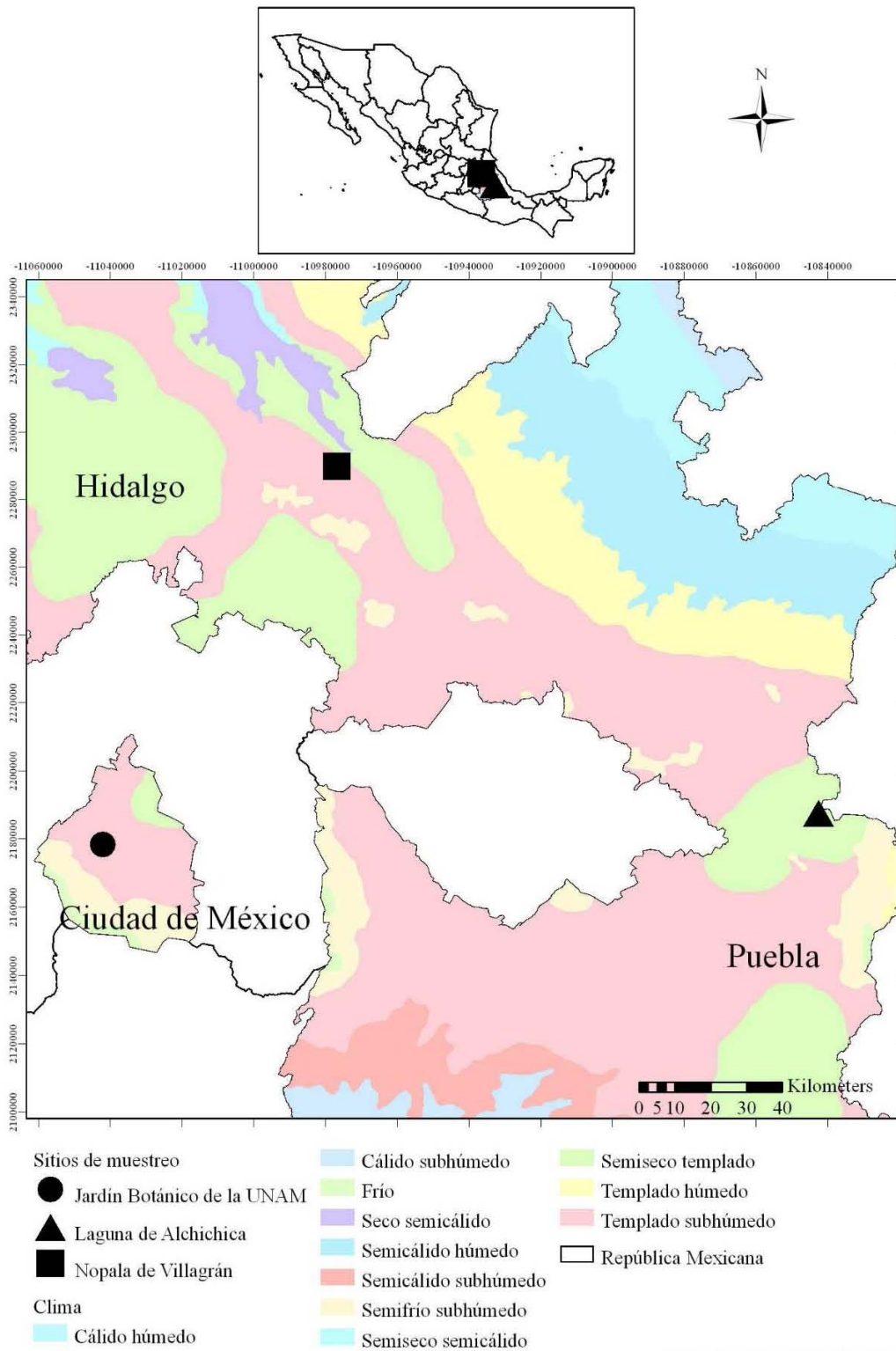Figura 2. Ubicación, uso de suelo y vegetación de cada área de muestreo.

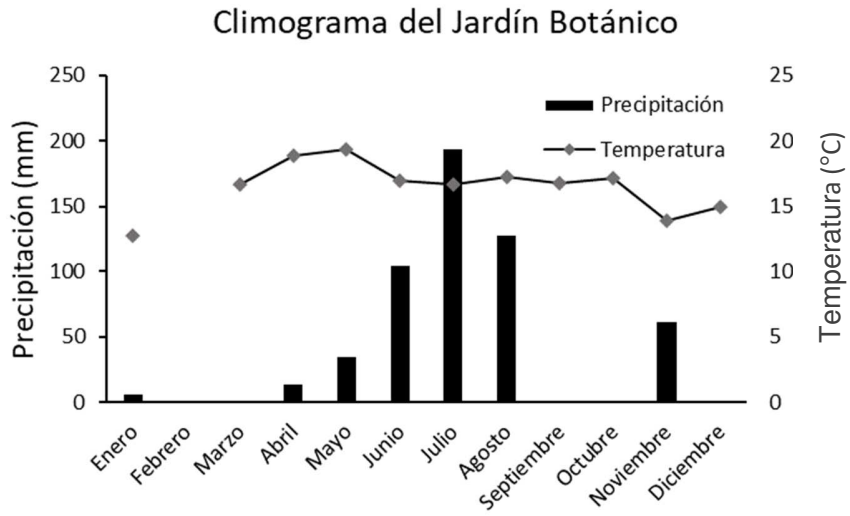Figura 3. Ubicación y clima de las tres áreas de estudio.

Figura 4. Climograma de la estación meteorológica CCH- S UNAM (19.3004 N, 99.2011 O) del Programa de

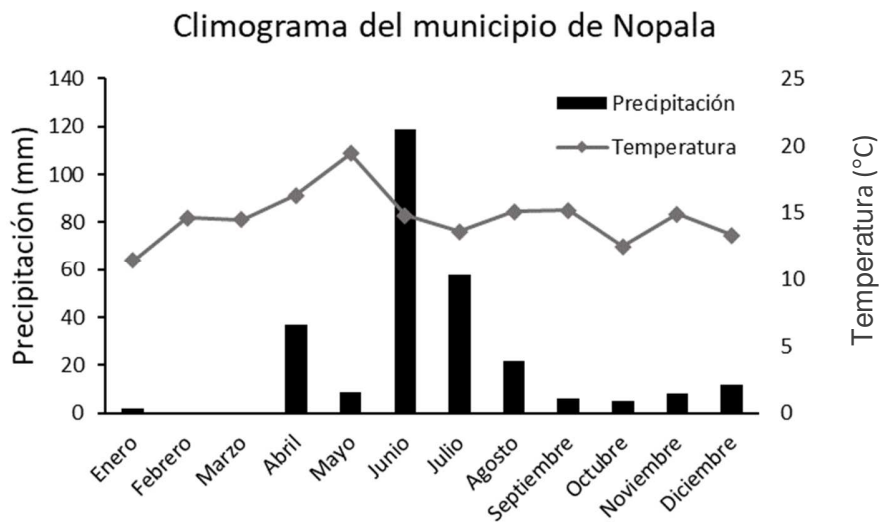Estaciones Meteorológicas del Bachillerato Universitario (PEMBU).

Figura 6. Climograma de la estación Maravillas del municipio de Nopala de Villagrán (20º 12´ 20.8˝ N, 99º

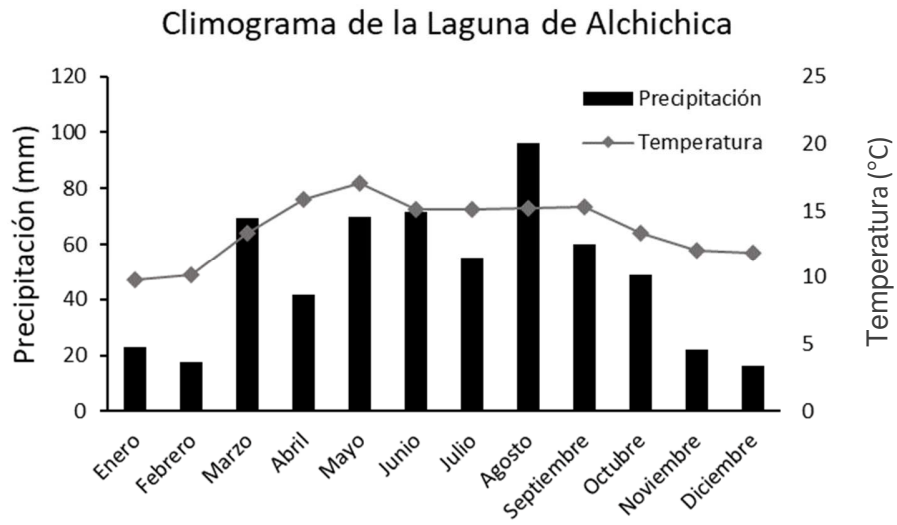35´ 15.69˝ O) de la Comisión Nacional del Agua (CONAGUA).

Figura 5. Climograma de la estación Alchichica de la Comisión Nacional del Agua (CONAGUA).