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Reproduction in *Sceloporus licki* (Reptilia: Phrynosomatidae) in the Cape Region, Baja California Sur

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Abstract
Sceloporus licki, an endemic lizard of the Cape Region from Baja California Sur, Mexico, shows evident sexual dimorphism in coloration and in snout-vent length between males and females. The gonadal analysis showed that both sexes have a synchronous spring–summer reproductive cycle. The males show maximum gonadal activity from March to July; in August, they show a rapid regression, and in September, quiescence is evident only in some males while in others recrudescence has already begun. Finally, in October and November, the process of recrudescence is obvious. The females showed some asynchrony, but for most, vitellogenesis occurred from April to June and eggs in the oviduct were evident in May, June and August. Oviposition occurs in July and August and by September or October there is no more gonadal activity in the ovaries. The clutch size was 5 ± 0.2 eggs, and hatchlings appeared in May–June and September suggesting that possibly two clutches are produced per breeding season. Reproductive activity in both sexes was like that of other lizards from temperate environments. However, the long period of gonadal recrudescence in both sexes (6 months) and rapid regression and quiescence in males of the studied population suggest plasticity in gonadal activity.

KEYWORDS
gonads, histology, reproduction, reproductive cycle, *Sceloporus licki*

1 | INTRODUCTION

Lizards of the genus *Sceloporus* inhabit a wide variety of environments, latitudes and altitudes. They include oviparous and viviparous forms and present different patterns of reproductive activity (Fitch, 1970; Guillette, Jones, Fitzgerald, & Smith, 1980; Méndez-de la Cruz, Villagrán-SantaCruz, & Andrew, 1998; Villagrán-Santa Cruz, Hernández-Gallegos, & Méndez-de la Cruz, 2009). The diversity in these patterns indicates that several biotic and abiotic factors influence and determine the moment in which this activity is carried out (see Granados-González et al., 2015; Villagrán-SantaCruz et al., 2014).

Although there have been several studies on reproductive cycles in oviparous species within different environments, in general, it has been determined that the reproductive activity of oviparous species in temperate areas is seasonal and is restricted to spring and summer. It is the most common pattern where reproductive events between both sexes occur synchronously (Bustos-Zagal, Méndez-de la Cruz, Castro-Franco, & Villagrán-Santa Cruz, 2011; Fitch, 1970; Goldberg, 2014; Guillette & Méndez-de la Cruz, 1993; Hernández-Gallegos et al., 2014; Méndez-de la Cruz, Villagrán-Santa Cruz, López-Ortíz, & Hernández-Gallegos, 2013; Villagrán-Santa Cruz et al., 2009). However, a few recent studies have shown that there is variation in the time, duration and intensity of the different gametogenic phases (see Granados-González et al., 2015, 2017). Although in recent years more emphasis has been placed on the knowledge of the reproductive cycles in Mexican species, the *Sceloporus* species of the Baja California Peninsula, especially those of the Cape Region in Baja California Sur have not been studied. Therefore, the objective of the present investigation was to determine the reproductive cycle in *Sceloporus licki*, by exploring the macroscopic and microscopic characteristics of gonadal activity, in order to precisely define the phases, time, duration and the main reproductive events that occur in this endemic species of the Cape Region.

Sceloporus licki taxonomically belongs to the *orcutti* complex within the *Sceloporus magister* group, in the Phrynosomatidae family (Wiens, Kuczynski, Arif, & Reeder, 2010). It is a species phylogenetically close to *S. orcutti* and *S. hunsakeri.* The first species is distributed to the north of the La Paz Isthmus, throughout the Peninsula; and the second one is also endemic to the Cape Region (Leache & Mulcahy, 2007; Wiens et al., 2010). Little is known about its basic biology, most studies on the species only consider general aspects of genetics (Hall, 1973), taxonomy and biogeography (Hall & Smith, 1979; Sites et al. 1992; Grismer & McGuire, 1996; Wiens & Reeder, 1997; Wiens et al., 2010), natural history (Grismer, 2002; Ramírez-Bautista & Arismendi, 2004), distribution patterns, habitat and conservation (López-Acosta, 2011), and thermal ecology and microhabitat use (Valdez-Villavicencio, 2013). *Sceloporus licki* is distributed from 300 to 1,700 masl in the mountainous areas of the Cape Region, from Rancho Ancón, south of La Paz, to Soledad in the Sierra La Laguna (Grismer, 2002). It is found in lowland deciduous forests and in pine–oak and oak–pine forests, as well as in the Sierra La Trinidad, southeast of the Sierra La Laguna (López-Acosta, Galina-Tessaro, Valdez-Villavicencio, & Peralta-García, 2016). It has been considered an arboreal species (Grismer, 2002; Hall & Smith, 1979), although it has been observed to prefer large rocks near trees and fallen trunks with abundant vegetation (López-Acosta, 2011). Information on reproduction in both sexes of this species is lacking with only one study documenting that the breeding season of this species occurs during the spring–summer period (Hall & Smith, 1979).

2 | MATERIAL AND METHODS

2.1 | Study area

The Cape Region, at the southern tip of Baja California Sur, between coordinates 24°21'24"N and 110°17'58.08 W" (on the La Paz Isthmus) and 22°52'29.25"N and 109°54'44.7 W", is one of the important biogeographic regions of the state due to the high number of endemism in plants and animals, particularly reptiles. The latter originated by its unique and complex geological history and the geographic isolation to which it was exposed during the Quaternary (Flores, 1998) period, which was caused by climatic changes as evidenced by various phylogeographic studies (Lindell, Méndez-de la Cruz, & Murphy, 2005; Lindell, Ngo, & Murphy, 2006). In this region, is located the only pine–oak forest of the Baja California Sur and the only deciduous lowland forest of the Baja California Peninsula, which occurs on the foot of the mountains, hills and canyons' slopes, in addition to the desert scrubland in the low-lands (Arriaga et al., 2000; León-de la Luz, Pérez-Navarro, Domínguez, & Domínguez, 1999). Its mountains are formed by outcrops of plutonic (granitic) rocks, while the foothills and plains are occupied by alluvial deposits (CONANP, 2003; Flores, 1998). In the high elevations of the Sierra La Laguna, the climate is mild sub-humid with rains in summer, while in the middle range dominates deciduous rainforest and its climate corresponds to warm steppes, meaning semi-arid (BS0 and BS1) with summer rains. There is a predominant summer–autumn (July–September) rainfall regime, accentuated by heavy showers or cyclones originated from the tropical Pacific, although there are also winter rains (December–February) or sleet to a lesser extent coming from humid systems from the north (Coria, 1988).

The study site for the present data was from the Cape Region in various sites with lowland deciduous forest, in the surroundings and low parts of the Sierra La Laguna and in the oak, oak–pine and pine forests in the high and middle parts of the same mountain range, where there are abundant areas with rocky outcrops that are used by *S. licki*.

2.2 | Fieldwork

As part of the research on distribution and ecology of *Sceloporus licki*, monthly during the period from 2009 to 2011, collection and observation of specimens was carried out via the noosing method and then sex and somatic measurements (snout-vent length—SVL, tail length, weight) were recorded. With the SVL data, the average, standard deviation (*SD*), and minimum and maximum values were obtained. A Mann–Whitney test was performed to compare sizes between sexes (Cooper & Vitt, 1989; Kaliontzopoulou, Carretero, Llorente, Santos, & Llorente, 2006; Ramírez-Bautista, Hernández-Salinas, Cruz-Elizalde, Lozano, & Rodríguez-Romero, 2016).

Some animals were analysed, and all of them were euthanized using an intraperitoneal injection of sodium pentobarbital (10%), following ethical norms for animal experiments and procedures for research at the Centro de Investigaciones Biológicas del Noroeste S.C. (CIBNOR) in La Paz, Baja California Sur. The specimens were fixed in 10% neutral

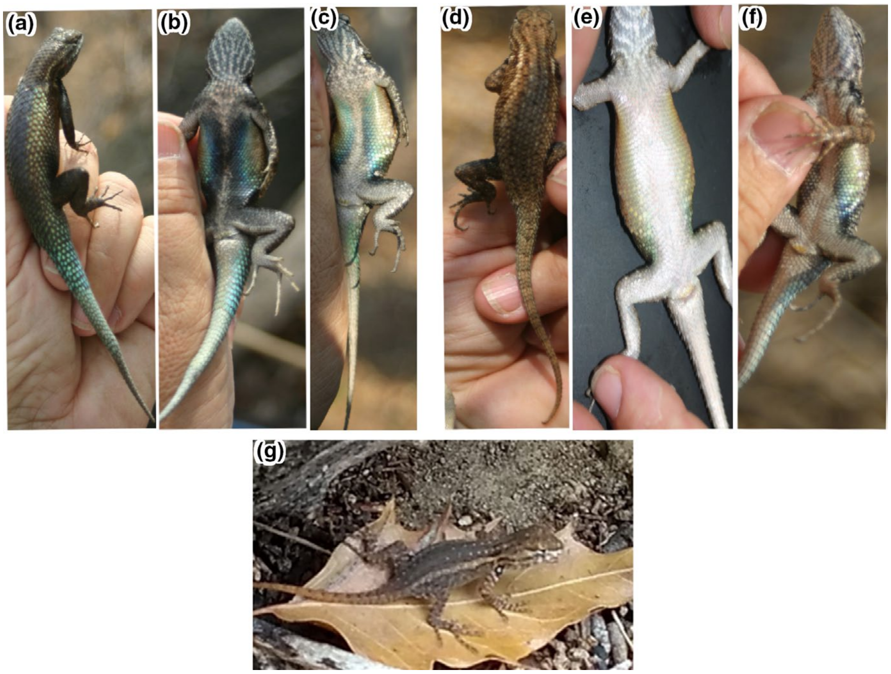

FIGURE 1 *Sceloporus licki* from the Cape Region, Baja California Sur. (a) Adult male dorsal view. (b) Adult male ventral view. (c) Juvenile male ventral view. (d) Adult female dorsal view and (e and f) Adult females ventral view. (Photos P. Galina). (g) Hatchling with the visible dorsolateral light stripe and the central light dot in the dark shoulder patch, characteristic of the species. (Photograph A. Cota)

buffered formalin, preserved in 70% ethanol and deposited in the Herpetological Collection of the CIBNOR.

2.3 | Laboratory work

Of the *S. licki* specimens already deposited in this collection, 49 adult males and females were selected covering the months of activity, during the spring, summer and autumn seasons (March–November). The right gonad and part of the excurrent duct (testicle—epididymis, ovary—oviduct) were extracted from each of the selected specimens, in order to observe the changes over time microscopically. A routine histological technique was performed, that included gradual dehydration in ethanol, xylene clearing, paraplast infiltration and embedding, 5 µm sectioning with a rotatory microtome and haematoxylin–eosin staining (Estrada, Peralta, & Rivas, 1982).

For males, the germinal cells (spermatogonias, spermatocytes, spermatids and mature sperm) were identified and classified according to Villagrán-Santa Cruz, Méndez-de la Cruz, and Parra-Gámez (1994), Villagrán-SantaCruz et al. (2014), and Rheubert et al. (2014). With an ocular micrometre under 40X magnification, the diameter of 25 seminiferous tubules and the height of the seminiferous epithelium in 25 random fields were measured, per specimen. From the measured parameters, individual average values were calculated for each specimen as well as monthly averages and the standard error. These data did not meet assumptions of normality; thus, non-parametric Kruskal–Wallis analysis was used to test for significant monthly variation in tubule diameter and seminiferous epithelial height. Analyses were performed using the Statistica, and a probability of 0.05 was used to determine significance in the analysed data.

The presence of sperm in the lumen of the seminiferous tubules and in the ducts of the epididymis was also determined. The observations were performed with an Olympus microscope; photomicrographs were taken with a digital camera and micrographs were created using Adobe Photoshop CS (Adobe Systems).

In addition to the size of the specimens (SVL), reproductive maturity was established microscopically by the presence of sperm in the lumen of the seminiferous tubules and in the epididymal ducts, in the smaller male specimens.

Females were analysed, in order to determine their reproductive condition, based on follicular development and the presence or absence of eggs in oviducts, and were classified as pre-vitellogenic females (with ovarian follicles <2 mm in diameter), vitellogenic females (with ovarian follicles >2 mm in diameter) and gravid females (with eggs in oviducts). The reproductive season was characterized by calculating the percentage of females in each reproductive condition per month. The size of sexual maturity was determined based on the size of the smallest female with eggs in the oviduct. The size of the clutch was determined by counting the number of eggs in the oviducts.

3 | RESULTS

Sexual dimorphism was observed in *Sceloporus licki*, as the SVL of males is greater and is statistically significant from those of females (Mann–Whitney U W = 502.5 p = 3.45e-6). As for colouring, adult males also have more colourful pigmentation, particularly in the gular and ventral regions (Figure 1). This coloration is more intense from June through September (Figure 1a,b). In the case of females, some specimens with faint ventral coloration like juvenile males were observed (Figure 1c,f). The average SVL in adult males was 73 ± 6.28 mm, with a maximum of 85.0 and a minimum of 62.8 mm ($n = 28$). The average SVL in females was 63.26 ± 4.04 mm, with a maximum of 72.0 and a minimum of 58.6 mm ($n = 21$).

From the analysis of a total of 49 specimens (28 males and 21 females), which were analysed in the months from March to November for males and from March to October for females, we can conclude that the *S. licki* population of the Cape Region in Baja California Sur presents a spring–summer seasonal synchronous reproductive cycle. It is evident that the maximum testicular activity and the presence of sperm in the lumen of the seminiferous tubules and in the epididymal ducts (from March to August) coincide with the presence of vitellogenic follicles, eggs in the oviduct and/or retention of sperm in the oviduct in females from April to August (Figure 2).

3.1 | Male reproductive cycle

Throughout the sampling months, we recorded significant changes in the diameter of the seminiferous tubules (Kruskal–Wallis; $H_{8,\,30} = 22.3$, $p = .004$, Figure 3a) and in the height of the seminiferous epithelium (Kruskal–Wallis; $H_{8,\,29} = 19.6$, $p = .01$, Figure 3b), as well as variation in the concentration of sperm in the seminiferous tubules and in the epididymal ducts (Figures 4 and 5).

The highest values in tubular diameter, as well as in the height of the seminiferous epithelium, occur in males collected in the months of March and April (Figure 3a,b), the histology of the gonads reveals that in March a high spermatogenic activity is already observed. All cell types of the spermatogenic process are seen, primary and secondary spermatocytes and mainly spermatids in spermiogenesis outlining the lumen of the seminiferous tubules and presence of sperm in the lumen, as well as in the lumen of the epididymal ducts (Figure 4a–d). In May, June and July, although the tubular diameter and height of the seminiferous epithelium decreases (Figure 3a,b), testicular activity remains with primary and secondary spermatocytes and spermatids in spermiogenesis and large amount of sperm in the lumen of the seminiferous tubules and epididymal ducts (Figure 4e–h), which shows that maximum reproductive activity occurs from March to July (Figures 2–4).

In the males collected in August, the testicle shows the indicative characteristics of regression: the diameter of the seminiferous tubules is significantly reduced (Figure 3a), as well as the tubular lumen. There is no longer spermatogenic activity; therefore, the height of the seminiferous epithelium is significantly reduced (Figure 3b). Only cellular remains of the process remain, and in the ducts of the epididymis, it is still possible to see some sperm (Figure 5a,b). In the gonads of males collected in September, the tubular diameters and the height of the seminiferous epithelium are low (Figure 3a,b). Histologically, in the seminiferous tubules of some males collected this month, it is possible to observe testicular quiescence; there is no lumen and only spermatogonia and nuclei of Sertoli cells in the tubular epithelium are

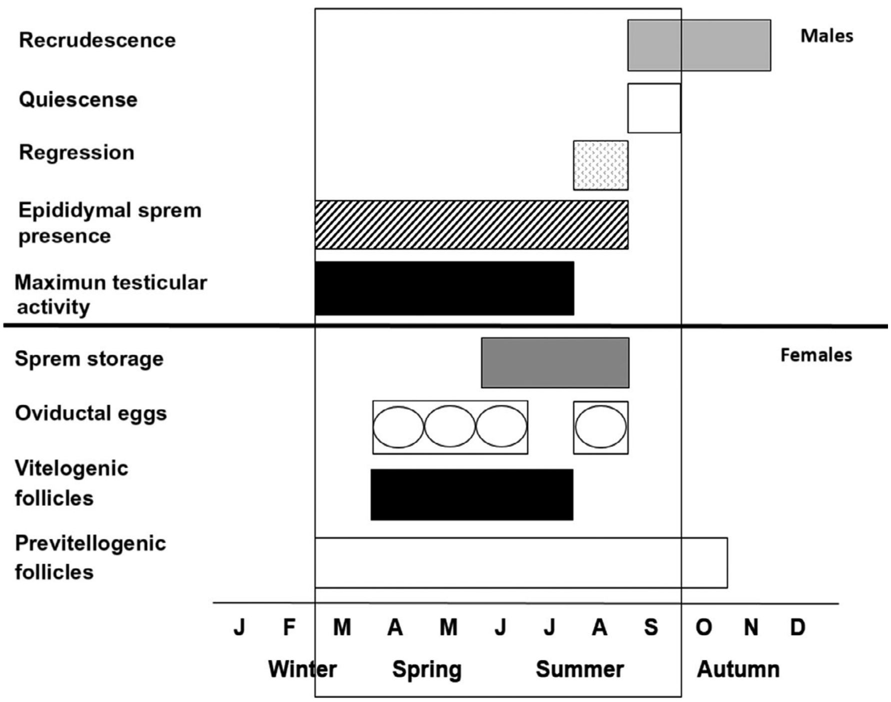

FIGURE 2 Diagrammatic representation of the reproductive cycle of *Sceloporus licki* males and females from a population found in the Cape Region, Baja California Sur. The box indicates the breeding season

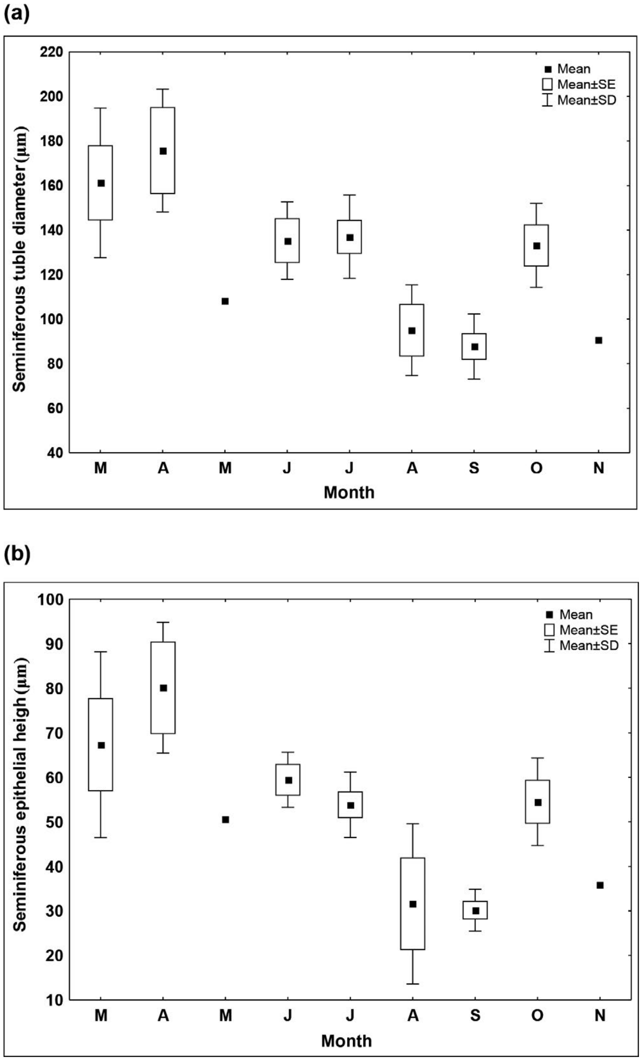

FIGURE 3 Monthly changes in seminiferous tubule diameter (a) and seminiferous epithelium height (b) throughout the reproductive cycle of *Sceloporus licki* from the Cape Region, Baja California Sur. Means and standard errors are represented

evident (Figure 5c). In the epididymal ducts, the diameter and height of the epithelium are markedly reduced and no sperm are observed (Figure 5d). In other males of the same month, testicular recrudescence is evident; in the seminiferous tubules, the tubular lumen is already observed and the proliferation of spermatogonia is remarkable, the epididymis is atrophied and no sperm are present (Figure 5e,f). In October and November, there is a significant increase in the diameter of the seminiferous tubules as well as in the height of the seminiferous epithelium (Figure 3a,b). Histology reveals in these months the progress of testicular recrudescence; with the proliferation of primary spermatocytes and the appearance of secondary spermatocytes (Figure 5g), the epididymis remains atrophied and devoid of sperm (Figure 5h). The smallest male with sperm in the lumen of the seminiferous and epididymal tubules was 62.8 mm in SVL, which was indicative of the size reached at sexual maturity.

3.2 | Female reproductive cycle

In the ovaries of *S. licki* females collected in March, we observed (100%) only pre-vitellogenic follicles (Figures 2,6 and 7), evident by their small size and histologically with theca's and characteristic follicular cells (small, medium and large or pyriform) and homogeneous cytoplasms, along with a few small atretic follicles (Figure 7a). In the April specimens, there is a similar proportion between vitellogenic females and females with eggs in oviducts. Females show vitellogenic follicles in different degrees of development, from initial vitellogenesis in some individuals, to advanced vitellogenesis in others and few females having follicles almost ready to ovulate (pre-ovulatory). It is notable that a female from this month, in addition to presenting follicles in initial vitellogenesis, also presents post-ovulatory follicles or luteal bodies, with theca's and luteal cell mass, which shows signs of luteolysis (some picnotic nuclei and vacuolated cytoplasm) (Figure 7b). It should also be clarified that this female presented eggs in her oviducts. The total number of females collected in May (100%) had eggs in oviducts (Figures 2 and 6); while in the ovary the post-ovulatory follicles or early luteal bodies formations are evident, indicating recent ovulation. Histologically, it is still possible to see the follicular cavity, which is being invaded by the proliferating follicular and theca cells and confirms the luteogenic phase (Figure 7c,d). In June, we found females with the three reproductive categories, 50% with pre-vitellogenic follicles, 25% with vitellogenic follicles and 25% were pregnant females with eggs in oviducts (Figures 2 and 6).

In July, females with pre-vitellogenic follicles predominated (75%) but we still observed females with follicles in late vitellogenic, almost about to ovulate (Figures 2 and 6), which are histologically characterized by their large size, homogeneous yolk, follicular cells and flattened theca cells (Figure 7e,f). In August, females with pre-vitellogenic follicles predominated (83.33%) and we observed the last females with eggs in their oviducts (16.47%) (Figures 2 and 6). During these last three months (June, July and August), the presence of retained sperm in the oviducts (no-glandular utero region) of females was evident (Figures 2 and 8a,b). In September and October, there was no reproductive activity (Figures 2 and 6), and we found females with very small ovaries where only atretic and pre-vitellogenic follicles were observed (Figure 7g); the latter are characteristic due to their theca cells, layer of follicular cells (large or pyriform, medium and small), homogenous cytoplasm and well-defined zona pellucida (Figure 7h). It is also noteworthy that in these last months, retained sperm are no longer observed in the oviducts (Figure 8c,d). The mean clutch size of *S. licki* in this study was five eggs (range 4–6 eggs/female). The smallest female with eggs in her oviducts had an SVL of 59.9 mm; and the smallest specimen with vitellogenic follicles in

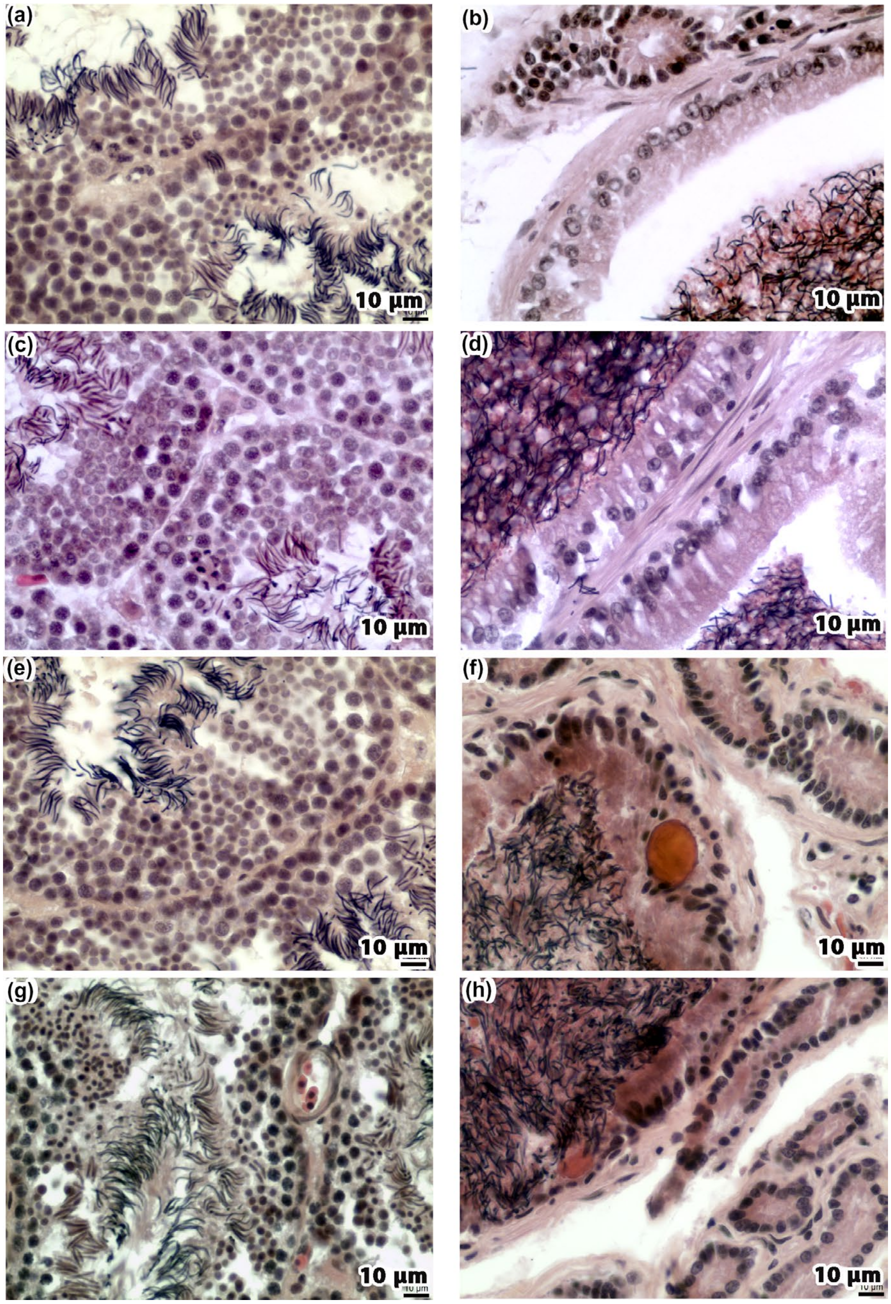

FIGURE 4 Period of the maximum testicular activity of the reproductive cycle of *Sceloporus licki*, from a population from the Cape Region, Baja California Sur. Seminiferous tubules is at its maximum activity with all cell types present and tall epithelial columns holding large cohorts of developing cells, numerous mature sperm can also be seen in the lumen or around the periphery of the lumen of the tubules in March (a), April (c), June (e) and July (g). Epididymal ducts showing the lumen filled with mature sperm in March (b), April (d), Jun (f), July (h). Haematoxylin–eosin stain

development and retained sperm had a 58.0 mm SVL. In May–June, the first offspring were observed in the field; they presented a 15 mm SVL and a dorsal–lateral stripe characteristic of the species (Figure 1d). The incubation period determined for most females covered less than two months.

4 | DISCUSSION

Sexual dimorphism was found in *Sceloporus licki.* In terms of SVL, males statically are larger than females, as in other species with this genus (Jiménez-Arco, Sanabria-Urbán, & Cueva del Castillo, 2017). Reptiles have different patterns of reproductive activity and these are reflected in gonadal changes and are one reason why reproductive phenology is an important aspect of their reproductive strategy (Fitch, 1970). It has been suggested for *S. licki* that the breeding season occurs during the spring–summer period (Hall & Smith, 1979); but in the present investigation, this information has been determined precisely by the histology of the gonads and their excurrent ducts. *Sceloporus licki* presents a reproductive cycle where maximum gonadal activity in both sexes occurs during the spring–summer period, which coincides with other species of oviparous sceloporids from temperate environments such as *S. orcutti* (Mayhew, 1963), *S. scalaris* (Newlin, 1976), *S. woodi* (Jackson & Telford, 1974), *S. occidentalis* (Goldberg, 1974), *S. graciosus* (Goldberg, 1975; Tinkle, Dunham, & Congdon, 1993), *S. spinosus* (Méndez-de

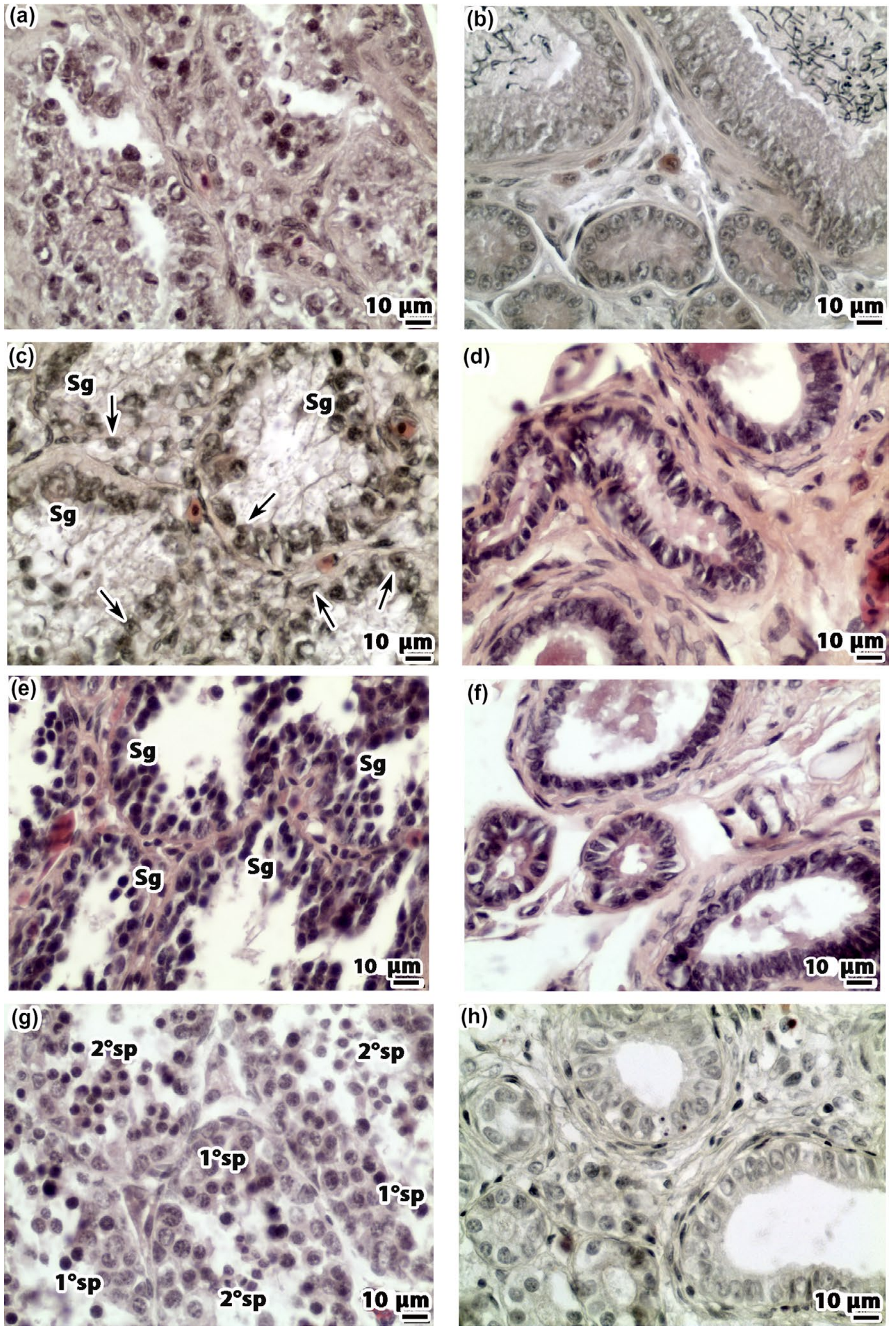

FIGURE 5 Gonadal and epidydimal changes throughout the reproductive cycle of *Sceloporus licki*, from a population from the Cape Region, Baja California Sur. (a–b) Regression (August). (a) Seminiferous tubules with germinal epithelium reduced in height. (b) Epididymal ducts partially filled with sperm. c – d Quiescence (September). (c) Seminiferous tubules only with spermatogonia (Sp) and Sertoli cells (arrows) present. (d) Epididymis with small ducts and lumen empty. (e–f) Start of Recrudescence (September). (e) Proliferation of spermatogonia in seminiferous tubules. (f) Epididymis without sperm. (g–h) Recrudescence (October–November). (g) The germinal epithelium with proliferation of primary (1° sp) and secondary spermatocytes (2° sp) observed close to the lumen. (h) Epididymis without sperm. Haematoxylin–eosin stain

la Cruz et al., 2013), *S. consobrinus* (Rheubert et al., 2014) and *S. aeneus* (Hernández-Gallegos et al., 2014). Reproductive phenology and reproductive activity in *S. licki* males are reflected in gonadal changes where the characteristic phases of every cycle are denoted, for example recrudescence or reactivation, maximum activity, regression and quiescence. In *S. licki*, it is notable that in males the gonadal reactivation occurs in September, and according to Rheubert et al. (2014) is a fall recrudescence with a prenuptial spermatogenesis, what coincides with other lizard species, such as *S. scalaris* (Newlin, 1976), *S. occidentalis* (Goldberg, 1974) and *S. woodi* (Jackson and Telford 1994). Within the *Sceloporus* genus, this is one of the spermatogenesis patterns; for example onset of spermatogenesis in summer/autumn, and generally occurs in species that inhabit temperate environments. Testicular recrudescence begins in September and vitellogenesis in females in the late winter, but the maximum gonadal activity coincides in both sexes in April and May (Rheubert et al., 2014). In *S. licki*, a long period of testicular recrudescence is evident, where spermatogenic transformation is gradually occurring and covers five to six months (from September to February), as has been observed in other species of oviparous or viviparous lizards from temperate environments; such as *S. aeneus* (Hernández-Gallegos et al., 2014) and *S. mucronatus* (Méndez-de la Cruz, Villagrán-SantaCruz, & Cuellar, 1994; Villagrán-Santa Cruz et al. 2009), respectively. In *S. licki,*

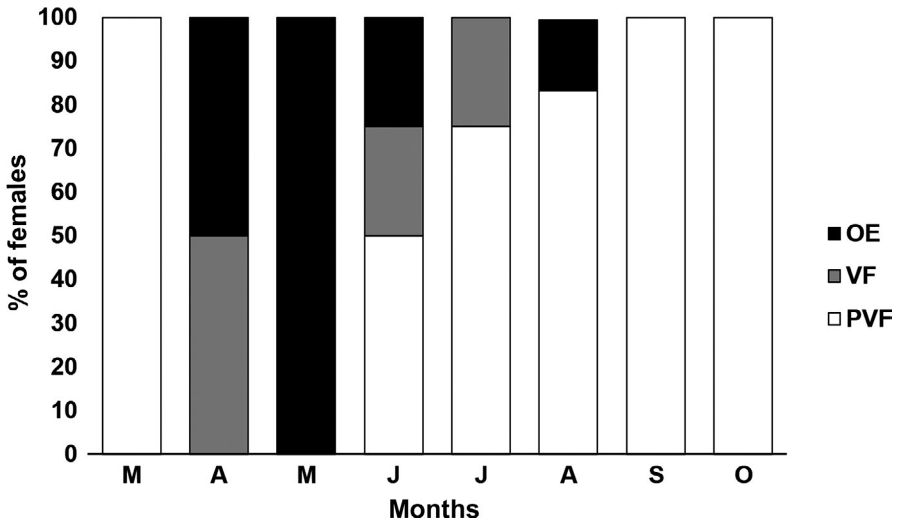

FIGURE 6 Monthly percentage changes in reproductive stages in female *Sceloporus licki* from the Cape Region, Baja California Sur: black bars, gravid females with oviductal eggs (OE); grey bars, females with vitellogenic follicles (VF), and white bars, females with pre-vitellogenic follicles (PVF)

maximum testicular activity occurs from March to July, in these months is evident an active spermiogenesis and presence of sperm in the tubular lumen, as well as in the epididymal ducts. In August, a rapid regression occurs and finally only in some September males is quiescence observed within the seminiferous tubules, as others have entered the phase of recrudescence or reactivation. It should be noted that the regression and quiescence phases in *S. licki* are very rapid and this occurs in the transition from August to September. In regression, the reduction in diameter of the seminiferous tubules is remarkable, as well as in height of the seminiferous epithelium. Few sperm are visible in the lumen of the seminiferous tubules and in the ducts of the epididymis in August. Quiescence is denoted by seminiferous tubules with reduced diameter and without lumen, and only spermatogonia and Sertoli cell nuclei are seen in the tubular periphery. These are typical characteristics that are also present in other species such as *Sceloporus spinosus* (Méndez-de la Cruz et al., 2013) and *S. aeneus* (Hernández-Gallegos et al., 2014). In *S. licki,* this rapid regression and quiescence is noteworthy since it has been observed as the typical phases of the spermatogenic cycles carried out in at least 2–8 months in other *Sceloporus* species (Granados-González et al., 2017), but it is compensated with a slow, long and gradual recrudescence and a considerable period of maximum testicular activity. The latter coincides with the record that, in warm climate species, the phases of spermatogenic activity are longer (Méndez-de la Cruz, Manríquez-Morán, Arenas-Ríos, & Ibargüengoitia, 2015). It is clear that in the gonadal cycles of male lizards, the four phases can occur at different times of the year (Méndez-de la Cruz et al., 2015); however, the moment in which it occurs, the duration and intensity of each phase is variable among species even in the same genus and sibling groups (Granados-González et al., 2017). In low-elevation, oviparous *Sceloporus* species, from tropical environments, present an extended period of maximum activity as in *S. variabilis*, which presents a unique cyclic pattern with an extended period of maximum activity (from November to July), with a rapid regression in August and apparently no quiescence (Granados-González et al., 2017; Peña-Herrera et al., 2018).

Reproductive cycles are strongly influenced by environmental conditions (Borrelli, De Stasio, Motta, Parisi, & Filosa, 2000; Grant & Dunham, 1990; Licht, 1984), which determine intraspecific reproductive variation when species occupy different habitats, altitudes or latitudes (Tinkle & Ballinger, 1972; Vinegar, 1975). All this environmental variability influence clearly supports that spermatogenic cycles are plastic and have evolved many times (Rheubert et al., 2014). However, some studies show that reproductive strategy is also influenced by phylogeny (Dunham & Miles, 1985; Mesquita et al., 2016), mortality (Peña-Herrera et al., 2018) and by the presence of available females (Gribbins et al., 2011).

It is evident that in the population of *S. licki* from the Cape Region, Baja California Sur, there are always females with ovaries in which pre-vitellogenic follicles are present, whether they are in reproductive activity or not. The vitellogenesis process, and the presence of post-ovulatory follicles or luteal bodies in the ovary, and the presence of eggs in oviducts, are indicative of reproductive activity within these female lizards. Vitellogenesis occurs from April to June in most females within this study; which coincides with other *Sceloporus* species from temperate environments, such as *S. scalaris* (Newlin, 1976), *S. occidentalis* (Goldberg, 1974) and *S. woodi* (Jackson & Telford, 1974). However, the presence of ovaries with post-ovulatory follicles and oviductal eggs in April for some females indicate that vitellogenesis and ovulation have previously occurred (February–March), which coincides with Rheubert et al. (2014), who state that vitellogenesis very possibly begins in the late winter, as occurs in other females of this genus. In June, there are still some females in the vitellogenic process, which surely continues through July, and finally into August, we can observe

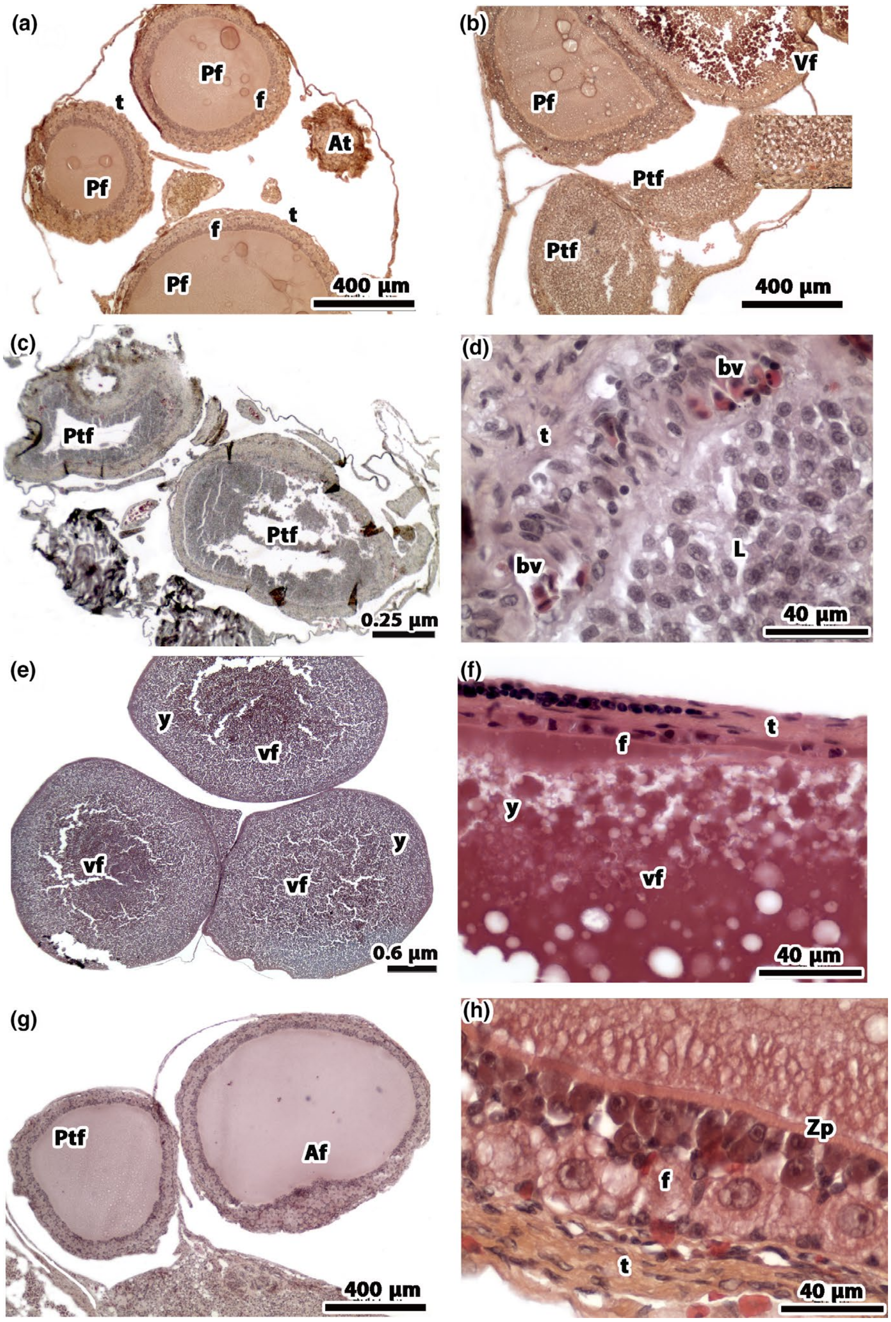

FIGURE 7 Gonadal changes throughout the reproductive cycle of female *Sceloporus licki*, from the Cape Region, Baja California Sur. (a) Pre-vitellogenic (Pf) and atretic follicles (Af) in ovary of a March female. (b) Pre-vitellogenic (Pf) and vitellogenic (Vf) follicles and evident post-ovulatory follicles (Ptf) in an ovary of an April female. (c) Early post-ovulatory follicles (Ptf) in ovary of a May female. (d) Higher magnification from the box of the previous image, with detail from post-ovulatory follicle, thecas (t), blood vessels (bv) and luteal cells mass (L). (e) Vitellogenic follicles (Vf) in ovary in July, the increased size of follicles was correlated with deposition of yolk (Y) within the cytoplasm and changes in the follicular wall. (f) Higher magnification from the box of the previous image, detail of the pre-ovulatory vitellogenic follicle wall, the follicular and theca cells are very thin. (g) Ovary from September with only pre-vitellogenic (Pf) and atretic follicles (Af). (h) Detail from a pre-vitellogenic follicle wall, thecas (t) and follicular cells (f) with three different cellular types (small, medium and big) and zona pellucida (Zp). Haematoxylin–eosin stain

the last females with eggs in the oviduct, to be laid possibly at the end of this month or in early September. Thus, we suggest that in this population, there is an asynchrony (when less than two months) between females in the processes of vitellogenesis, ovulation and oviposition which still coincides with the rain season, and therefore with the greater environmental productivity. In oviparous lizards, ovulation and oviposition often occur within a short-deferred time frame of one to three months (Méndez-de la Cruz et al., 2013), and according to Goldberg (1971) and Ballinger (1973), eggs are laid when hatching time favours the survival of newborns.

In most *S. licki* females, ovulation and the consequent formation of post-ovulatory follicles in the ovary, and the presence of eggs in oviducts in April, May, June and even August indicates the production of a clutch during the breeding season. One clutch per breeding season is a common phenomenon in several lizard species (Fitch, 1985). However, *S. licki* females from this population show a long breeding season (of at least six months), so it is possible that in this period some females can start reproductive activity earlier than others and have two clutches per season, as suggested for oviparous species with long breeding seasons and with short gestational periods (Andrews & Mathies, 2000; Dunham, Miles, & Reznick, 1988; Vitt & Breitenbach, 1993). It has been hypothesized that the frequency of clutches is associated with the length of the breeding season, and in tropical habitats where the breeding season is long, multiple clutches are favoured (Vitt & Breitenbach, 1993). The other alternative to

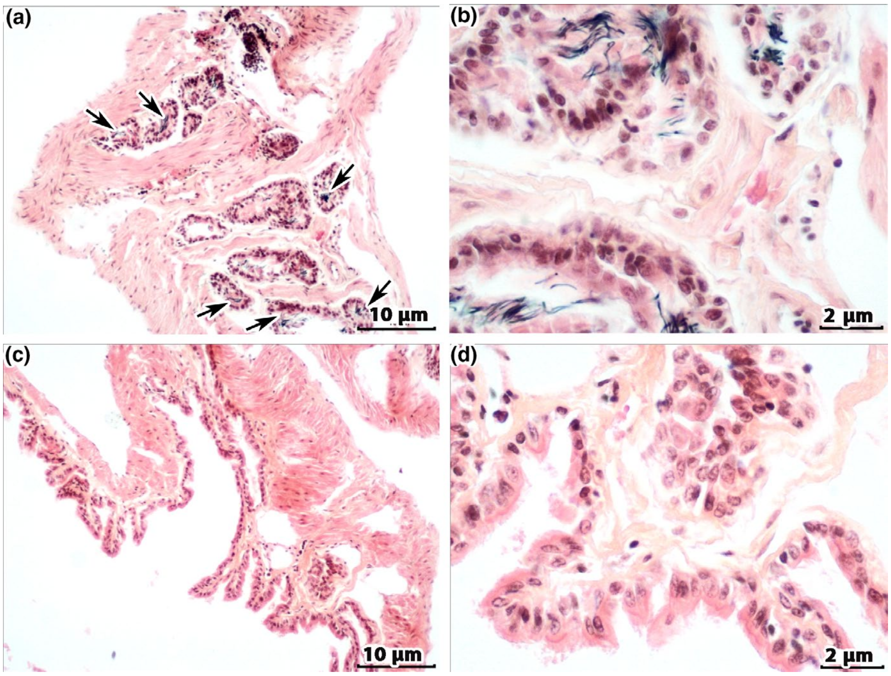

FIGURE 8 Photomicrographs of non-glandular uterus of *Sceloporus licki*, from a population from the Cape Region, Baja California Sur. (a) Transverse section of non-glandular uterus showing sperm storage receptacles (arrow) with presence of sperm from a female collected in July. Haematoxylin–eosin stain. (b) Higher magnification from the box of the previous image. (c) Transverse section of non-glandular uterus without evidence of sperm retention of a female collected in September. (d) Higher magnification from the box of the previous image without sperm storage. Haematoxylin–eosin stain

explain the presence of eggs in oviducts in those months is that some other females start this process late and breed late into the season, what supports the asynchronous among them within the population. The asynchrony in *S. licki* from this study population determines that some females may have early offspring in May and June. The ovulation of most females occurs in April and May, the eggs present in the oviduct in May and June and oviposition occurs in July, at the end of the dry season and the beginning of the rainy season. The offspring are finally observed in September still in the rainy season. Some females lay late clutches at the end of August or early September and the appearance of the offspring occurs even later. This opens the possibility that some females of *S. licki* within this population may present a clutch at the beginning of the breeding season and the other clutch at the end of it or simply breed later in the season. It has been argued that the production of early and late clutches can be the result of reaching sexual maturity at different times of the year (López-Moreno et al., 2016; Rubio-Blanco, 2007).

In *S. licki,* the evidence of post-ovulatory and vitellogenic follicles in ovary and oviductal eggs in the month of April in some females reveals on one hand that post-ovulatory follicles are the result of a process of vitellogenesis and previous ovulation, that should have started at least two or three months before, which is reflected in a first clutch, confirmed by the presence of offspring in the field in the May and June months. On the other hand, the presence of vitellogenic follicles indicates that the maturation of a second group of follicles has begun, which will possibly give a second clutch perhaps in late August or early September.

Our study also shows that the average clutch size, obtained from the number of eggs in the oviduct, in *S. licki* was five. The variation in clutch size is an important characteristic of the reproductive effort and has been documented in many species (Fitch, 1978, 1985). Lizards that produce a single clutch usually produce larger egg numbers than those that produce multiple clutches (Mattison, 1989). In *S. licki*, the size of the clutch may be low, because there may be a possibility for a second clutch during the breeding season. The time period between incubation, oviposition and offspring observation is less than two months. Hatching occurs when conditions are appropriate and food resources are abundant, during and after the rainy season, which could therefore be determining the number of clutches in a year.

Reproductive activities in both sexes of *S. licki* were similar to that of other lizards from temperate environments, where testicular recrudescence begins in September and vitellogenesis in females occurs in late winter, but the maximum gonadal activity in the majority of lizards regardless of sex coincides together in spring/summer (Rheubert et al., 2014). The reproductive phenology of oviparous *Sceloporus* females seems to be highly conserved at different altitudes, but in males, the shortness of regression and quiescence phases may change, as in the population of the present study. How in some other *Sceloporus* species, the long period of gonadal recrudescence in both sexes (6 months) and the rapid regression and quiescence of *S. licki* of the studied population suggest plasticity in gonadal activity.

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