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**Cover Page Footnote**

I thank Christine Thacker (LACM) for permission to examine specimens.;

## Reproduction of the Yellow-backed Spiny Lizard, *Sceloporus uniformis* (Squamata: Phrynosomatidae) from California

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The reproductive cycle of *Sceloporus uniformis* was studied by a histological examination of gonads collected from five California counties: Inyo, Kern, Los Angeles, Riverside and San Bernardino. Males followed a testicular cycle in which sperm production (spermiogenesis) started in March and was completed by August. The smallest reproductively active male measured 79 mm SVL. Females were reproductively active from March into July. Mean clutch size ( $n = 21$ ) was  $6.48 \pm 2.2$  SD, range = 3–10. The smallest reproductively active female (enlarged follicles  $> 5$  mm) measured 78 mm SVL. Histological evidence is presented (oviductal eggs and concomitant yolk deposition) that multiple clutches are produced by some females of *S. uniformis*.

The yellow-backed spiny lizard, *Sceloporus uniformis* Phelan and Brattstrom, 1955, occurs primarily in the Mojave and Great Basin Deserts of California, Nevada, Utah, and northwestern Arizona, as well as the Central Valley of California from near sea level to around 1,520 m (Conrad 2009). Schulte et al. (2006) elevated the subspecies *Sceloporus magister uniformis* to *Sceloporus uniformis*. Previous information on its reproductive cycle are one or more clutches of 4–19 eggs deposited from May to August (Conrad 2009). In Nye County, Nevada, a mean of 7.0 eggs was produced (Tanner and Krogh 1973). In southern Utah (Washington County), reproduction occurs from May to July with two clutches averaging 6.2, range 2–9 eggs (Tinkle 1976). Five adult *S. uniformis* females from the Providence Mountains, San Bernardino County, California collected between May 22 and June 11 contained enlarged ovarian follicles (Johnson et al. 1949). The purpose of this paper is to provide additional information on the reproductive cycle of *S. uniformis* from a histological examination of gonads. Categorization of the reproductive cycle including period of sperm production, timing of yolk deposition and number and sizes of clutches produced provides important information in formulating conservation policies for lizard populations (Gibbons 1994). Due to the difficulty in obtaining collecting permits for large collections of monthly lizard samples, utilization of museum collections for obtaining reproductive data has become increasingly important.

A sample of 239 *S. uniformis* consisting of 105 adult males (mean SVL = 100.8 mm  $\pm$  9.6 SD, range: 78–124 mm), 51 adult females (mean SVL = 91.5 mm  $\pm$  7.6 SD, range: 77–108 mm), 75 juveniles (mean SVL = 56.3 mm  $\pm$  10.6 SD, range: 37–56 mm) and eight neonates (mean SVL = 32.1 mm  $\pm$  4.0 SD, range: 24–34 mm) collected 1921 to 1980 was examined from the herpetology collection of the Natural History Museum of Los Angeles County (LACM), Los Angeles, California, USA (appendix).

The left gonad was removed and embedded in paraffin. Histological sections were cut at 5  $\mu$ m and stained by hematoxylin followed by eosin counterstain (Presnell and Schreibman 1997). Enlarged follicles  $> 5$  mm length and oviductal eggs were counted. Histology slides were deposited in LACM. The snout-vent length (SVL) of each specimen was measured from the tip of the snout to the posterior margin of the vent. An unpaired

Table 1. Monthly stages in the testicular cycle of 105 *Sceloporus uniformis* from California.

Month	N	Regression	Recrudescence	Spermiogenesis
February	1	0	1	0
March	14	0	10	4
April	25	1	2	22
May	28	0	2	26
June	14	2	0	12
July	9	8	0	1
August	8	6	1	1
September	1	0	1	0
October	5	1	4	0

*t*-test was used to compare *S. uniformis* male and female mean body sizes (SVL) and the relationship between clutch size and female SVL was examined by linear regression analysis utilizing Instat (vers. 3.0b, Graphpad Software, San Diego, CA).

Mean body size (SVL) for adult males was significantly larger than for adult females (unpaired *t* test,  $t = 6.1$ ,  $df = 156$ ,  $P < 0.0001$ ). Three stages were noted in the testicular cycle: (1) Regression, germinal epithelium is greatly reduced in size and consists of 1–3 layers of spermatogonia and interspersed Sertoli cells; (2) Recrudescence, a proliferation of germ cells occurs in preparation of the upcoming period of sperm formation; primary and secondary spermatocytes predominate. Spermatids are common in late recrudescence. (3) Spermiogenesis, lumina of the seminiferous tubules are lined by sperm and/or clusters of metamorphosing spermatids. Stages in the testicular cycle by month are in Table 1. The main period of spermiogenesis occurred in April–June. *Sceloporus uniformis* with regressed testes predominated in July–August. Testicular recrudescence initiated in summer and was completed the following spring (Table 1). The smallest reproductively active male (spermiogenesis) measured 79 mm SVL (LACM 17242) and was collected in Los Angeles County during March.

Four stages were noted in the ovarian cycle of *S. uniformis* (Table 2): (1) Quiescent, no vitellogenic granules are noted in the ooplasm; (2) Early yolk deposition, basophilic yolk granules in the ooplasm; (3) Enlarged ovarian pre-ovulatory follicles ( $> 5$  mm); (4) Oviductal eggs. The period of ovarian activity extended from March into July. Mean clutch size for 21 gravid females of *S. uniformis* is  $6.48 \pm 2.2$  SD, range = 3–10. The smallest reproductively active female (three enlarged follicles  $> 5$  mm) measured 78 mm SVL (LACM 17252) and was collected in Los Angeles County in June. Linear regression analysis revealed a significant positive correlation between female SVL ( $n = 21$ ) and clutch size ( $Y = -6.25 + 0.138X$ ,  $r = 0.512$ ,  $P = 0.018$ ). There was evidence that some *S. uniformis* females produce multiple clutches in the same reproductive season as both LACM 63819 from Kern County collected in March and LACM 96089 from San Bernardino County collected in May contained oviductal eggs and concomitant yolk deposition for a subsequent clutch.

*Sceloporus uniformis* exhibits a testicular cycle with timing typical of many other phrynosomatid lizards from western North America in which spermiogenesis occurs in spring, followed by late summer regression and recrudescence (recovery) initiated in autumn and completed the following spring (Goldberg 1974, 1975, 1977). Likewise, the ovarian cycle of *S. uniformis* is similar to that of many other North American temperate zone phrynosomatid lizards which initiate yolk deposition in the spring and complete it in summer with one or two egg clutches produced (Goldberg 1974, 1975, 1977).

Table 2. Monthly stages in the ovarian cycle of 51 *Sceloporus uniformis*: from California. \*LACM 4516 and \*\* LACM 17251 contained damaged follicles or oviductal eggs that could not be counted.

Month	N	Quiescent	Early yolk deposition	Enlarged follicles > 5 mm	Oviductal eggs
March	7	1	4	0	2
April	11	2	5	4	0
May	10	2	1	2	5*
June	14	5	1	4**	4
July	6	4	0	0	2
August	1	1	0	0	0
September	1	1	0	0	0
October	1	1	0	0	0

*Sceloporus uniformis* of presumed neonate sizes (24, 28, 30 mm SVL) first appeared in July. They were also collected in August (34, 34, 35 mm SVL) and September (33, 35 mm SVL). The appearance of hatchlings in July is earlier than appearance of *S. uniformis* hatchlings in Utah which first appeared in August (Tinkle 1976). However, Tanner and Krogh (1973) reported hatchlings of *S. uniformis* appeared in late July in Nevada.

Previous reports on clutch sizes in *S. uniformis* from Utah mean = 6.2, range = 2–9 (Tinkle 1976), and Nevada mean = 7.0 (Tanner and Krogh 1973) are close to the mean of 6.5 range = 3–10 reported herein. The reports of larger clutch sizes (18, 19 respectively) for *S. uniformis* are from field guides (Stebbins 1954; Lemm 2006; Stebbins 2003; Conrad 2009) and likely reflect *Sceloporus magister* sensu stricto, not *S. uniformis*. There is a report of 19 eggs from *S. magister* from Maricopa County, Arizona in another field guide (Brennan and Holycross 2005). Also, males of *S. magister* reach maturity at 95 mm SVL (Parker and Pianka 1973) as opposed to 79 mm SVL reported for *S. uniformis* herein.

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## Appendix

*Sceloporus uniformis* from California examined from the herpetology collection of the Los Angeles County Museum of Natural History (LACM), Los Angeles County, California.

**Inyo:** 36665, 52996, 27182, 27183, 75267, 123376, 123377.

**Kern:** 8570, 27184, 63817–63824, 63827, 63828, 69816, 69865, 69867, 69869, 95989, 95990, 95991, 23378.

**Los Angeles:** 4516, 4517, 4521, 4522, 4523, 17135, 17222, 17224–17227, 17233–17238, 17242–17244, 17277, 17251–17254, 17263, 17264, 27186, 27189, 52937, 61874, 74180, 95992–95995, 123375.

**Riverside:** 17276, 22269–22274, 22276, 22278, 22279, 22281, 22283, 22285, 22286, 22288–22298, 22300–22312, 22316, 22318, 22320, 22322, 22323, 22325, 22326, 52938, 52940, 52942, 73568, 73569, 73572, 73574, 73579–73581, 73583, 73683, 95998–96000, 96002, 96003, 96005, 96006, 96012, 96016, 96017, 96020–96022, 96027, 96028, 96031, 96035, 96038, 96041, 96044, 96046, 96047, 96050, 96052, 96055–96057, 96113, 138085.

**San Bernardino:** 4526, 4527, 17132, 17136, 17265–16267, 17271, 17274, 17275, 21653, 21654, 21657–21659, 21661, 22277, 22278, 22313, 23254, 23258–23267, 36587–36590, 63814–63816, 63826, 64003, 64004, 67317, 74200, 96061, 96063, 96065–96067, 96069, 96072, 96073, 96076, 96078–96084, 96086, 96087, 96089, 96091–96096, 96098, 96100, 96105, 96106, 96108, 96111, 96117, 96123, 96124, 96127, 96131, 96132, 115620, 115622, 115623, 115625, 122058, 122432, 122433, 123375, 171372, 171376.