NOTES ON THE ECOLOGY OF THE IGUANID LIZARD, *SCELOPORUS MAGISTER*

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ABSTRACT: Desert spiny lizards were studied at nine different localities between Mojave, California and Estero de Tastiota, Sonora, Mexico, from 1963 to 1970. The species is usually arboreal in association with a wide variety of trees or large cacti, but is sometimes terrestrial or saxicolous. Food consists primarily of ants and adult beetles. Adults consume a wider range of different-sized prey, contain more food items per stomach, and eat more of the smallest food items than do smaller lizards. Females >80 mm SVL are mature. Fourteen gravid females were collected from April to early August and contained an average of 8.4 eggs/clutch. Males mature at about 95 mm SVL and have enlarged testes from April to mid-June. Seasonal changes of abdominal fat bodies were irregular in females, but a gradual increase in fat body size occurred from spring to late summer in adult males, and a decrease during the same period in immatures. Body temperatures of active lizards in nature are maintained over a fairly narrow range (30.3–37.8 C) and average 34.8 C. Mean preferred body temperature of 6 lizards was significantly higher (36.7 C vs. 34.5 C) in a thermal gradient chamber after 2 months under laboratory conditions at 20–25 C. Older, larger lizards have higher frequencies of broken regenerated tails than smaller ones. The life history of *S. magister* appears closer to *S. orcutti* than to *S. clarki* or *S. olivaceus* among members of the *spinosus* group.

THE desert spiny lizard, *Sceloporus magister* Hallowell, is a frequently uncommon, but widely distributed desert lizard in western North America. No one has studied its ecology in any detail, however, and what is known about this species is scattered through numerous publications. Here we consolidate the diffuse literature on *S. magister* and present some new information on

its ecology from our own studies. Aspects of its ecology are briefly compared with those of other members of the *spinosus* group (*S. clarki, olivaceus,* and *orcutti*) and other ecologically well known species in the genus.

Miscellaneous observations on the natural history of *S. magister* were made by Ruthven (1907), Van Denburgh (1922), Smith

(1939, 1946), Cowles (1941), Johnson et al. (1948), Shaw (1952), Milstead (1953), Stebbins (1954), Gates (1957), Minton (1959), Banta (1962a), Miller and Stebbins (1964), Pianka (1965, 1966, 1967), Asplund (1967), and Montanucci (1968). Ruthling (1917), Knowlton (1934, 1938), Eaton (1935), and Knowlton and Thomas (1934) examined its diet. Hotton (1955) related diet to dentition, and Johnson (1966) calculated energy assimilation. Color changes and relationships were examined by Atsatt (1939) and Norris and Lowe (1964). Body temperature relationships have been treated variously by Cowles and Bogert (1944), Bogert (1949a, b), Taylor and Tschirgi (1960), Brattstrom (1965), and McGinnis and Falkenstein (1971). Endoparasites were described by Wood (1935) and Telford (1970a). Hearing was investigated by Peterson (1966) and Campbell (1969), and geographic variation was described by Phelan and Brattstrom (1955). The zoogeography and possible past movements of *S. magister* in the Great Basin desert were considered by Banta (1962b); Brattstrom (1953) described Pleistocene fossils of this species. Fitch (1970) reviewed what is known about reproduction in *S. magister*.

STUDY AREAS AND METHODS

Observations were made on over 140 *S. magister* during the springs and/or summers of 1963, 1964, 1965, 1966, 1968, 1969, and 1970 in southern California, Arizona, southern New Mexico, and the Mexican state of Sonora. Much of our information is based on 133 specimens which were actually collected and preserved, although our discussion of microhabitat utilization patterns also incorporates a few animals that escaped. Lizards were collected on 9 geographically separated study areas at latitudes of 35° 06′ N (M), 33° 41′ N (W), 33° 26′ N (SM), 32° 57′ N (C), 31° 50′ N (EP), 29° 54′ N (PL), 29° 38′ N (B), 29° 22′ N (H), and 28° 20′ N (A). Area EP includes mesquite-yucca associations between 1–75 km west of El Paso, Texas, in Doña Ana and Luna counties, New Mexico. Descriptions of and data on the climate,

fauna, and flora of the other areas are available elsewhere (Pianka, 1965, 1966, 1967, 1970; Parker, 1972; Pianka and Parker, 1972).

For most lizards encountered, we recorded: date, time, approximate size (small, medium, or large), sex (if possible), and microhabitat position in the environment when first observed. Many lizards were also collected; this material provided additional data on cloacal temperature, sex, wet weight, exact size (snout-vent length, SVL), and whether or not the tail had been broken and regenerated. All SVL and tail lengths were measured on live, or freshly killed lizards in the field. Testes dimensions and fat body lengths of preserved specimens were measured with vernier calipers or millimeter rulers, and ratios of mean testis width to SVL were calculated to compensate for differences in body size. In some preserved males the terminal end of the vas deferens was removed, crushed, and examined for spermatozoa. Some testes from area EP were sectioned at 10 μm and stained with Ehrlich's hematoxylin and eosin. Volumes of intact stomachs were estimated to 0.1 cc by volume displacement. Estimates were made of the numbers and volumes of items in various prey categories for each stomach. Approximate volumes of individual prey items were estimated visually to the nearest 0.01 cc, by the proportion of the total stomach volume taken up by a given item. Age terminology follows Pianka and Parker (1972).

Preferred body temperatures (PBT) of several lizards were recorded within two weeks of capture in a thermal gradient chamber similar to that described by Licht et al. (1966). Lizards were run again after they had been held in captivity for over 2 months in order to assess the degree of acclimation to laboratory conditions and the stability of PBTs. Heat lamps were turned on at 0600 h and off at 1800 or 2000 h each day. The thermal gradient was located in an air-conditioned room at 20–25 C. Lizards were fed mealworm larvae every morning. A telethermometer and recorder were set to monitor BTs for 1 min at 4-min inter-

vals, a rate of 15 measurements per hour. Depending upon how long an individual was monitored, the number of PBT measurements for any given specimen varied from 96 to 193 per day. Most lizards were monitored for an entire day's activity cycle. Means, standard deviations, and standard errors of the mean were computed from these data for individuals for each day's trace.

RESULTS AND DISCUSSION

Habitat and Microhabitat.—S. magister occupies many different habitat types in various parts of its extensive geographic range, including rocky areas in canyons and foothills as well as typical flatland desert habitats (Bogert, 1949a). Although it is usually arboreal, associated with trees such as cottonwood, willow, mountain ash, mesquite, paloverde, ironwood, and yucca (Smith, 1939; Milstead, 1953; Gates, 1957), it is also found on the ground in some habitats (Smith, 1939, 1946; Stebbins, 1954). In still other habitats, it is primarily saxicolous (Johnson et al., 1948; Stebbins, 1954).

On most of our study areas, S. *magister* was distinctly arboreal, being associated with a variety of large desert plants including Joshua trees, paloverde, ironwood, smokethorn, and various species of cacti including saguaro, organ pipe, *Pachycereus*, and *Opuntia*. We regularly found these lizards in pairs (one male and one female) in trees along desert washes, especially those with packrat nests underneath them. Of 82 undisturbed lizards with microhabitat data when first sighted, 69 (84.2%) were in or underneath trees. They are exceedingly wary and very adept at staying on the side of a branch opposite the human observer; we found that pairs of people working together were most effective in collecting specimens. Individuals are seldom far from a safe retreat, either a hole in the ground, a packrat nest, or a hollow in a tree. On areas PL and EP, lizards were decidedly terrestrial. On area EP they were sometimes seen basking on rocks or piles of railroad ties, but were usually on the ground under or near large mesquite bushes, and

TABLE 1.—Summary of stomach contents of 123 *Sceloporus magister* from 8 study areas in southwestern United States and northwestern Mexico.

Prey category	Number	Volume	% Total number	% Total volume	Frequency*
Spiders	10	0.57	0.13	0.41	9
Solpugids	3	2.57	0.04	1.83	3
Pseudoscorpions	3	0.01	0.04	0.01	2
Isopods	2	0.12	0.03	0.09	2
Ants	6319	32.62	79.70	23.21	83
Other Hymenoptera	37	3.78	0.47	2.69	22
Grasshoppers	12	1.90	0.15	1.35	12
Roaches	9	1.15	0.11	0.82	4
Mantids	3	0.70	0.04	0.50	3
Lacewings	1	0.10	0.01	0.07	1
Adult beetles	716	71.04	9.03	50.56	97
Hemiptera	21	1.44	0.26	1.02	17
Diptera	9	0.73	0.11	0.52	6
Adult Lepidoptera	1	0.10	0.01	0.07	1
All insect larvae	253	10.92	3.19	7.77	46
Unidentified insects	38	2.35	0.48	1.67	27
Vertebrates	1	0.50	0.01	0.36	1
Plant materials	281	7.67	3.54	5.46	31
Unidentified materials	4	1.85	0.05	1.32	11
Nematodes	205	0.37	2.59	0.27	4
TOTALS	7928	140.52			

* Number of stomachs containing item indicated.

generally retreated into packrat nests when disturbed.

Diet.—Table 1 shows that the species is a relatively generalized feeder, taking a fairly wide variety of arthropod prey. Numerically, ants are by far the most abundant items, followed by adult beetles and insect larvae. Volumetrically, adult beetles are most prominent, followed by ants and plant materials (secondarily ingested?). Our data are in close agreement with those of Knowlton (1934, 1938).

Detailed food habits are poorly known for most *Sceloporus*. In the *spinosus* group, S. *olivaceus* eats mostly Orthoptera, Lepidoptera larvae, and Hemiptera (Kennedy, 1956). Another large species, S. *poinsetti*, preys primarily upon Orthoptera and plant material (Smith and Milstead, 1971). The smaller S. *occidentalis* is somewhat closer to S. *magister*, with its diet being dominated numerically by ants, termites, Diptera, and Coleoptera (Johnson, 1965).
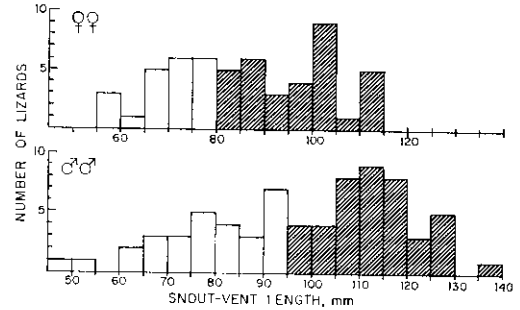
TABLE 2.—Prey size distribution in three size groups of *Sceloporus magister*.

Prey size (cc)	Small (32–80 mm)		Medium (81–100 mm)		Large (101–140 mm)	
	N	%	N	%	N	%
Small (0.002–0.008)	329	58.0	1300	83.0	4432	92.0
Small-medium (0.01–0.09)	212	37.4	234	14.9	240	5.0
Medium (0.1–0.9)	26	4.6	33	2.1	139	2.9
Large (1.0–1.4)	0	0.0	0	0.0	5	0.1
Totals	567		1567		4816	
Number of stomachs	40		36		47	
Average number of prey/stomach	14.2		43.5		102.4	

FIG. 1.—Body sizes (SVL) of male and female *Sceloporus magister* showing sexual dimorphism in size. Cross-hatching indicates adults.

Comparison of prey size with body size in *S. magister* shows differential utilization of different sized prey among three size groups (Table 2). Surprisingly, the diet of smaller lizards is about equally balanced between small and small-medium prey, whereas the largest lizards consume small items (mostly ants) almost exclusively. Number of items per stomach also increases dramatically with body size. This may be correlated both with the dietary shift and with increased stomach size. Smaller lizards may eat more larger items either because they are less efficient than older, more experienced ones, and therefore have to expend more energy per prey capture, or because they are exposed to a different spectrum of available prey in different microhabitats than adults.

Size, Growth, and Maturity.—Sexual size dimorphism is moderate. Males achieve somewhat larger sizes than females (Fig. 1), and are also marked by dark coloration (blue or black) on throat and lateral chest and abdomen.

Hatchlings may appear from late June through September in various parts of the geographic range. Hatchlings are approximately 32–33 mm SVL (size of smallest individuals collected) and may grow 20 mm

or more before winter (largest autumn juvenile was 55 mm). Size of one-year olds apparently varies widely, the smallest being about 58 mm in June and July, and 67 mm in August.

The smallest gravid female was 81 mm, and the smallest male with enlarged testes during the breeding season was 95 mm. Comparison with studies of two other *Sceloporus* in the *spinosus* group, *S. olivaceus* (Blair, 1960), and *S. orcutti* (Mayhew, 1963a, b), shows minimum adult size in *S. magister* is close to *S. orcutti* in males, and similar to both species in females (Table 5). Most *S. magister* may take at least two to three years to reach minimum adult size, judging from the progressive increase in size of first year lizards from about 50 mm in spring to about 80–90 mm in autumn. The earliest sexual maturity would thus be at an age of about 22 months, most similar to the slow-maturing *orcutti*.

Age structure in *S. magister* is heavily weighted toward adults. Mortality in eggs and/or hatchlings may be high since we collected only 3 individuals smaller than 40 mm. This implies that the species has a high adult longevity and low juvenile survivorship. Our entire sample of 133 lizards is composed of 31% adult males, 24.4% adult females, 37% immatures, and only 7.4% young-of-the-year. Alternatively, the low number of small lizards could be due to differences in their habits and/or microhabitats, reducing their visibility or availability for collection. In addition, few

of our samples were from autumn when juveniles would possibly be most abundant.

Reproduction.—Females contained yolked ovarian follicles >4 mm in diameter from April to early August. Oviducal eggs were found only in May and June. Yolk deposition probably begins in April and first clutches are laid between mid-May and late June. Some females may lay more than one clutch. One from area EP contained both oviducal eggs and 2 yolked ovarian follicles (4.0 mm) on 29 May 1970. Gravid females were found as follows: 2 of 2 in April, 3 of 5 in May, 6 of 15 in June, 1 of 3 in July, and 1 of 6 in August. One hatchling appeared on area SM on 30 June 1966.

Mean clutch size in 13 gravid females, plus 1 with fresh corpora lutea, was 8.4 (3–12). Mean for 5 oviducal and corpora lutea counts was 8.2 (7–11). Gravid females averaged 98.8 (81–112) mm SVL. Larger females generally had larger clutches. Seven small females (81–99 mm SVL) averaged 7.4 (5–10) eggs per clutch, whereas seven larger ones (100–112 mm SVL) had 8.7 (3–12) eggs per clutch.

Surprisingly, smaller females appear to have a higher reproductive effort than larger ones. Two small females (81 and 87 mm SVL) had an average effort (total wet weight of oviducal eggs/total weight) of 25.9%, whereas 2 larger females (both 102 mm SVL) averaged 16.5%—about 60% of the effort exhibited by the small females. This difference was not influenced by clutch size since the 2 smaller females each had 7 eggs, while the 2 larger ones averaged 10 (9 and 11).

The gross reproductive cycle of male *S. magister* is basically similar to that of other temperate iguanids such as *Sceloporus undulatus* (Altland, 1941), *Uta stansburiana* (Asplund and Lowe, 1964), and *Sceloporus orcutti* (Mayhew, 1963a), but differs from those of some other *Sceloporus* such as *S. jarrovi* (Goldberg, 1971) and *S. occidentalis* (Wilhoft and Quay, 1961). *S. magister* testes are enlarged from April to mid-June. Decline in testicular size is rapid between late June and July. Testes are quiescent in August and apparently begin enlarging
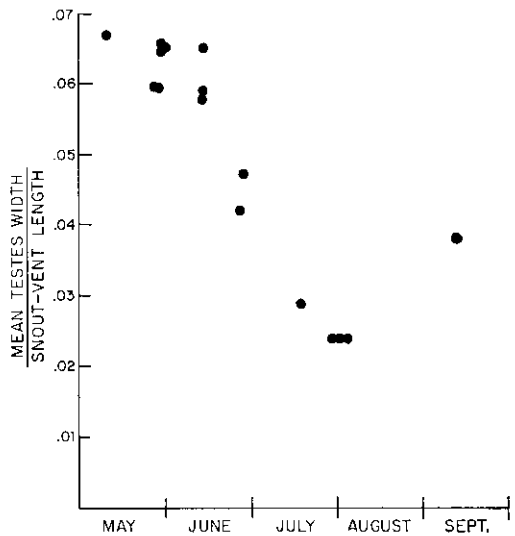

FIG. 2.—Seasonal changes in relative testis size of adult male *Sceloporus magister* from area EP. Each dot represents the mean of both testes for one male.

again in September. A sample of 16 adult males from area EP illustrate these changes (Fig. 2). Males from area EP had spermatozoa in the terminal end of the vas deferens from early May through July. Some May and all August–September males lacked spermatozoa. Males collected on other study areas conformed to this basic testicular pattern, indicating a rather restricted spring breeding period in May and June. Using the histological testicular stages of Licht (1967), the testes of 4 males from area EP were in stage 6 on 10 May and 13 June, in stage 1 on 1 August, and in stage 3 on 7 September.

Abdominal Fat Bodies.—For analysis of seasonal changes in fat body size, lizards were placed in one of four groups: 1) reproductive adult females, gravid or with fresh corpora lutea; 2) non-reproductive adult females, with no evidence of recent reproduction; 3) adult males; and 4) immatures, all lizards below minimum adult sizes. Changes in fat bodies of both categories of females were irregular and showed no consistent trends (Fig. 3). We expected reproducing females to have smaller fat
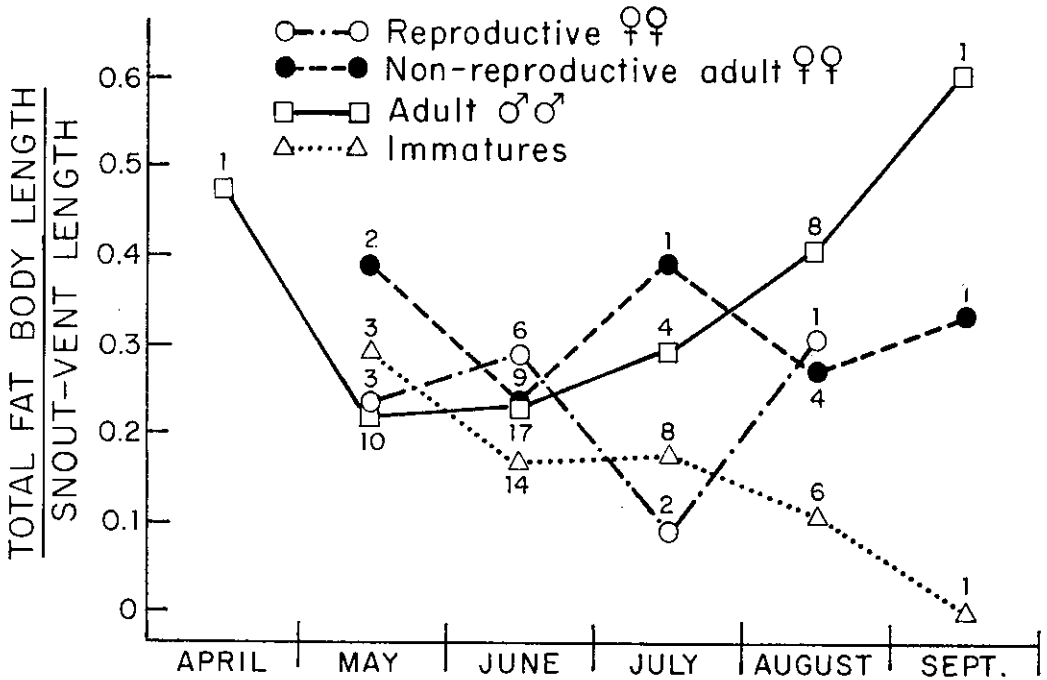
FIG. 3.—Seasonal changes in relative size of abdominal fat bodies in four sex and size classes of *Sceloporus magister*. Numbers in parentheses are the number of lizards on which the means are based.

bodies than non-reproducing individuals, but we found no consistent difference. Adult males showed a rather clear trend of increasing fat body size from a May low to a September peak. Immature lizards, however, exhibited the reverse trend, with fat body size decreasing consistently from May through September. This decrease may be partially due to inclusion of juveniles in late summer samples, resulting in depression of the mean. Other inconsistencies presumably arise from combining samples collected over a wide geographic area as well as from different years.

In contrast to our results, Hahn and Tinkle (1965) and Telford (1970b) found a significant reduction of abdominal fat bodies during reproduction in females of *Uta stansburiana* and *Takydromus tachydromoides*, respectively. The seasonal pattern of male fat bodies of these species was, however, generally similar to S. *magister* in showing a gradual increase in late summer and autumn.

Thermoregulation.—Fig. 4 shows the frequency distribution of body temperatures (BT) of 92 active S. *magister* ($\overline{X} = 34.8$ C, $s = 1.63$), with the mean being identical to the value reported by Brattstrom (1965) and almost identical to Bogert's (1949a) 34.9 C. There is a weak positive, but statistically insignificant, correlation between air temperature and body temperature ($r = 0.178$), which always exceeds air temperature, often by as much as 10 C. There is no significant difference between the mean BT of animals in the sun when first sighted and those in the shade.

The BT activity range for S. *magister* is somewhat narrower than for other sympatric iguanids such as *Callisaurus draconoides* (Pianka and Parker, 1972), *Dipsosaurus dorsalis* and *Phrynosoma platyrhinos* (Pianka, 1965; Pianka and Pianka, 1970), and much narrower than it is in some other *Sceloporus* species (Brattstrom, 1965). Pianka (1965) suggested that this may be a reflection of the arboreal habits of the species, since
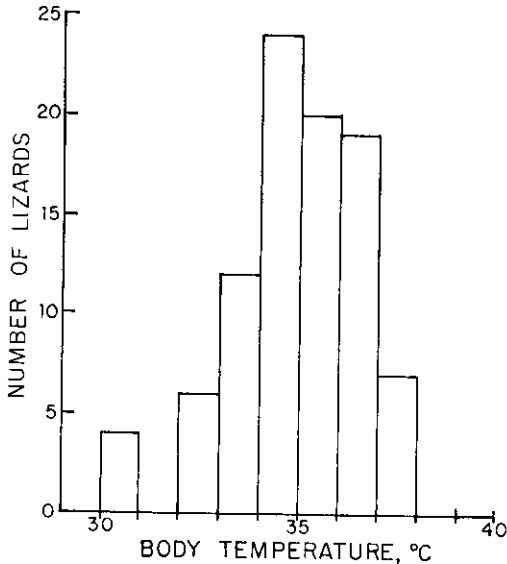
FIG. 4.—Frequency distribution of body temperatures of 92 active *Sceloporus magister*.

TABLE 4.—Frequencies of broken regenerated tails by size class and sex for *Sceloporus magister*.

Size class (SVL)	N	Number broken	Percentage broken
Juveniles			
32–60 mm	8	3	37.5
61–80 mm	31	4	14.2
Females			
81–100 mm	19	7	36.9
101–120 mm	14	4	28.6
Males			
81–100 mm	20	4	20.0
101–120 mm	28	13	46.4
121–140 mm	8	4	50.0

individuals would only have to shift position slightly to be in the sun or shade, or on a warmer or cooler substrate. Moreover, they do not normally move through a diverse thermal environment, seldom expend energy making long runs, and thus do not raise

TABLE 3.—Preferred body temperature statistics for *Sceloporus magister*, before and after acclimation to laboratory conditions. N = number of recordings. Each line represents one individual. Overall before statistics, based on four individuals; overall after statistics, on six.

Date	$\overline{x}$	SE	s	N
June 13	34.77	.107	1.38	165
June 20	36.32	.092	1.15	156
June 25	32.61	.081	1.13	193
June 26	34.89	.146	1.75	143
Overall before	34.53*	.075	1.93	657
August 26	37.69	.112	1.10	96
August 27	37.90	.080	1.03	166
August 28	37.49	.053	.70	172
August 29	37.15	.095	1.24	170
August 30	34.94	.087	1.13	169
September 3	34.54	.077	.78	101
Overall after	36.69*	.056	1.65	874

* Significantly different at .001 level.

their BT metabolically. *Urosaurus graciosus*, another arboreal species in the flatland desert, also has a low variance in BT (Pianka, 1965). It would be interesting to know whether terrestrial populations of S. *magister* maintain more variable body temperatures than arboreal ones.

Table 3 gives PBT statistics for individuals from each day's trace and overall statistics separated into two groups: those recorded soon after capture and those obtained 2 months later, after the lizards had opportunity to acclimate to laboratory conditions. The mean PBT before and after is significantly different (t-test, $P < .001$) but mean PBT before is not significantly different from the mean for field animals. Wilhoft and Anderson (1960) and Mueller (1970) reported acclimation in *Sceloporus occidentalis* and *Sceloporus graciosus*, respectively. S. *magister* acclimated at relatively low laboratory conditions (20–25 C) exhibited an increase in PBT, the reverse of Wilhoft and Anderson's (1960) results which showed a lowering of PBT after acclimation to high temperature (35 C).

Predation.—The frequency of broken regenerated tails increases with size (Table 4), perhaps because older lizards have had more contacts with predators. Males have slightly higher frequencies than females, possibly reflecting aggressive territorial behavior of males, or perhaps greater exposure to predators by males during their normal daily activities. Samples are too small to

TABLE 5.—Comparison of major aspects of reproduction in species of the *spinosus* group of the genus *Sceloporus*.

Species	Location	Mean clutch size	No. of clutches	Period of egg laying	Time of maximum testis size	Age at maturity	SVL at maturity (mm)		Author
							♂♂	♀♀	
clarki	Arizona & Mexico	12.0	11	May–Nov	—	—	—	73	Fitch (1970)
magister	Western USA & Mexico	8.4	14	May–Aug	May–Jun	2–3?	95	81	present study
magister	Western USA & Mexico	12.4	8	May–Jul	—	—	—	—	Fitch (1970)
olivaceus	Texas	14.3	28	May–Jul	—	1	65	80	Blair (1960)
orcutti	California	11.0	4	May–Jul	Apr	2–3	90	85	Mayhew (1963a, 1963b)

detect possible latitudinal trends in predation intensity as indicated by broken tails.

Comparison with Related Species.—Data are available for three other species in the *spinosus* group of *Sceloporus*. Comparison with S. *magister* shows all four species are generally similar in clutch size and a spring-early summer breeding period (Table 5). The most notable differences are the extended egg laying of S. *clarki* and the early maturity and small size of males in S. *olivaceus*. Clutch sizes in the *spinosus* group are consistently larger than those of smaller oviparous *Sceloporus* in other groups: *graciosus*, 3.8 (Fitch, 1970); *occidentalis*, 7.7 (Fitch, 1970); *undulatus*, 7.6 (Crenshaw, 1955). These differences may reflect the larger body size in the *spinosus* group, allowing production of larger clutches.

Clutch size apparently varies widely within S. *magister*. Our mean and range are considerably below those reported by Fitch (1970), perhaps due to geographic variation, sizes of females in samples, or annual meteorological factors influencing egg production. Further conclusions and comparisons must await more extensive collections and more intensive population studies of these large *Sceloporus* species.

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