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Ecology of *Sceloporus undulatus speari* (Sauria: Phrynosomatidae) from North-Central Chihuahua, Mexico

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We studied the ecology of a population of *Sceloporus undulatus speari* from the Transmontane Sand Dune region of northern Chihuahua, México. Most of the individuals in our population used fence posts or yucca plants as perches and were only rarely seen on the ground. The majority of individuals in our population were seen in full sun, although a substantial number were in shade. Mean body temperature in our population was 35.2°C. Individuals first seen in full sun had lower T_b s than individuals first seen in shade. Lizards using different microhabitats (e.g., yucca vs. fence post) had different body temperatures. Clutch size in our population was 5.23 eggs per clutch. Clutch size in our population was not statistically significantly related to female body size; however, the trend was for an increase in clutch size with SVL, with the smallest females having the smallest clutches. We found no evidence for sexual dimorphism in body size (SVL) in our population of *S. undulatus*, but males had larger heads. Coleopterans (particularly tenebrionids) and hymenopterans (particularly formicids) were the most important prey items.

Studying populations of species with large geographic ranges can provide answers to questions regarding the relative roles of genetics and the environment in determining variation in ecological traits (e.g., life history, thermal physiology, demography). Perhaps no other species of lizard has received as much attention in this regard as *Sceloporus undulatus*, which has been the subject of numerous statistical and theoretical analyses of geographic variation in life-history traits (e.g., Tinkle and Ballinger, 1972; Tinkle and Dunham, 1986; Gillis and Ballinger, 1992; Adolph and Porter, 1993, 1996; Niewiarowski, 1994; Smith et al., 1996). More recently, populations of *S. undulatus* have been the focus of more experimental investigations into the causes of such geographic variation (e.g., Ferguson and Talent, 1993; Niewiarowski and Roosenburg, 1993; Niewiarowski, 1995, 2001; Angilletta, 2001a,b).

Although *S. undulatus* has served as a model organism for studying geographic variation, much of the information used in these analyses has come from North American populations and subspecies. Relatively little detailed information is known about the biology and ecology of the Mexican populations and subspecies of *S. undulatus* (but for studies on *Sceloporus belli*, formerly *Sceloporus undulatus belli* in Durango, México, see Barbault et al., 1978; Barbault and Maury, 1981; Gadsden-Esparza and Aquirre-León, 1993). We studied a population of *Sceloporus undulatus speari* from the Transmontane sand dune region of northern Chihuahua, México. Our objective was to provide additional information on the understudied populations and subspecies of *S. undulatus* in México so that future synthetic studies of *S. undulatus* ecology have greater geographic representation.

MATERIALS AND METHODS

Our study site was located at the Rancho El Setenta, Municipio Juárez (31°13'34.9"N, 106°30'29.7"W; 1282 m elevation) in northern Chihuahua, México. The study area lies within the transmontane sand dunes area located on the windward sides (south and west) of the Samalayuca, El Presidio, and associated mountain ranges. At our study site, the sand dunes are semistabilized with numerous fence posts and yucca (*Yucca filifera*).

Lizards were collected by hand or by using rubber bands in July and August of 1998 and 1999. We recorded the microhabitat and the amount of sunlight (e.g., sunny vs. shaded) where the lizard was first seen. Upon capture, we measured body temperature (T_b) to nearest 0.1°C using a quick-reading cloacal thermometer. We measured snout–vent length (SVL) to the nearest 1 mm using a plastic ruler.

Lizards were collected by hand and preserved shortly after collection (initially in 10% formalin, and finally in 70% ethanol; deposited in the herpetological collection of the Laboratorio de Ecología of the Unidad de Biología, Tecnología y Prototipos). Measurements were then made on each individual including SVL, maximum head width (HW) and head length (HL; from anterior edge of ear to tip of snout). Snout–vent length was measured to the nearest 1 mm with a ruler, and all remaining variables were measured to the nearest 0.01 mm using dial calipers. Sex was determined by checking for the presence of enlarged anal scales in males.

We later dissected the lizards, making observations on the stomach contents and reproductive status of females. Diet items were identified to the lowest feasible level, typically or-

der or family. Volumes of prey items were estimated by volumetric displacement (to nearest mm³). We also calculated Simpson's Diversity Index ($1/\sum p_i^2$) to examine diet breadth. Clutch size was determined by dissection of females and counting enlarged follicles or oviductal eggs.

We used only sexually mature males and females in our analysis of sexual dimorphism. Based on our dissections (see below), females appear to mature at about 41 mm SVL, so we used 39 mm as a conservative estimate of sexual maturity in males and females. Analyses of sexual dimorphism in body parts (e.g., head width, head length) were conducted using Analysis of Covariance with SVL as the covariate, and using log-transformed data. Unless a significant interaction term in the ANCOVAs is noted, the interaction term was not significant and was thus removed from the final model. Means are given ± 1 SE.

RESULTS AND DISCUSSION

Microhabitat Use. — The majority of lizards were first seen perching on fence posts (60 of 103; 58.3%). A significant number were found perching on yucca plants (36 of 103; 35.0%). Lizards were occasionally found on bushes (1), walls (1), the ground (1), mesquite trees (2), and railroad ties (2).

In nearly two-thirds of the cases, lizards occupied sunny microhabitats (41 of 64; 64.0%), with the rest occurring in the shade. Waldschmidt (1980) observed shifts in the proportion of *Sceloporus undulatus elongatus* in a Colorado population in full sun and full shade with changes in thermal conditions, suggesting that these lizards are using perches in sun and shade to behaviorally thermoregulate. In a Missouri population, *Sceloporus undulatus hyacinthinus* in the middle of the summer use perches in the shade or sun/shade mosaic more than perches in the full sun; however, early and late in the activity season, they use perches in full sun more frequently (Angert et al., 2002).

Body Temperature. — Mean T_b was $35.2 \pm 0.2^\circ\text{C}$ (range = 29.2 – 39.8°C ; $N = 102$). Males and females had similar T_b s (male: $35.2 \pm 0.2^\circ\text{C}$, $N = 60$; female: $35.3 \pm 0.3^\circ\text{C}$, $N = 42$; $F_{1,100} = 0.171$, $P = 0.68$). These values fall within the range of body temperatures observed in other populations of *S. undulatus* (range 27.9 – 36.8°C ; Crowley, 1985; Gillis, 1991; Grover, 1996; Angilletta, 2001b).

Individuals in sunny microhabitats ($35.0 \pm 0.4^\circ\text{C}$, $N = 40$) had significantly lower T_b s than individuals in shaded microhabitats ($36.2 \pm 0.2^\circ\text{C}$, $N = 23$; $F_{1,61} = 5.83$, $P = 0.019$). A similar pattern was found in a Utah population of *S. u. elongatus*, where individuals found in full sunlight had a substantially lower mean T_b than those in full and partial shade (Grover, 1996). Presumably this pattern reflects thermoregulatory shuttling by these lizards to maintain a particular T_b (see Waldschmidt, 1980).

We limited our analysis of the effects of microhabitat use on temperatures to yucca and fence posts since the number of sightings of lizards on other microhabitats was too small for statistical analysis. Lizards using fenceposts ($35.9 \pm 0.2^\circ\text{C}$, N

= 59) had higher T_b s than lizards using yucca ($34.0 \pm 0.4^\circ\text{C}$, $N = 36$; $F_{1,93} = 28.5$, $P < 0.0001$). These results, along with those for sun exposure, suggest the probability that these lizards behaviorally thermoregulate by adjusting their location.

Clutch Size. — Mean clutch size was 5.23 ± 0.35 eggs (range = 3–8; $N = 26$). Mean SVL of females from which clutches were obtained was 53.3 ± 1.4 mm. The smallest female with enlarged follicles or oviductal eggs was 41 mm SVL. This is the lowest clutch size yet reported for a population of *S. undulatus* (range 5.5–11.8; reviewed in Smith et al., 1996). The fact that our population has the smallest clutch size is consistent with the observation that our population also has the smallest size at maturity among the studied populations (range = 45–66 mm; for review, see Smith et al., 1996).

Clutch size increased with SVL with the two smallest females only having clutches of three eggs; however, the regression only approached statistical significance and the amount of variation in clutch size explained by SVL was fairly low ($N = 26$; $r^2 = 0.13$, $P = 0.076$; $CS = 0.62 + 0.087$ SVL).

Sexual Dimorphism. — Males (50.90 ± 0.54 mm, $N = 123$) and females (50.38 ± 0.80 mm, $N = 89$) were not significantly different in SVL ($F_{1,210} = 0.31$, $P = 0.58$). The extent of sexual dimorphism in body size varies among populations of *S. undulatus*. Sexual dimorphism varied among seven subspecies of *S. undulatus*, with some subspecies showing large differences between male and female size (e.g., *S. u. elongatus*, females larger) and others with relatively little difference in the sizes of males and females (e.g., *Sceloporus undulatus conso-brinus*, females slightly larger; Fitch, 1978). A recent experimental analysis suggests that sexual dimorphism in body size in some *S. undulatus* populations is based on differences in the growth rates of juvenile males and females (Haenel and John-Alder, 2002).

Males (10.46 ± 0.13 mm, $N = 123$) had wider heads than females (9.93 ± 0.14 mm, $N = 89$; sex term: $F_{1,208} = 18.1$, $P < 0.0001$), and the relationship between SVL and HW differed between males and females, with male HW growing faster than female HW (SVL \times sex interaction term: $F_{1,208} = 19.5$, $P < 0.0001$). Males (9.61 ± 0.10 mm, $N = 123$) had longer heads than females (9.28 ± 0.14 mm, $N = 89$) but the difference was not quite significant ($F_{1,209} = 5.70$, $P = 0.018$). We are not aware of other studies on head size dimorphism in *S. undulatus*, which is quite surprising. Additional study of head size dimorphism in other populations of *S. undulatus* could allow for an examination of geographic variation in the intensity of sexual selection. Other species of *Sceloporus* show geographic variation in head size dimorphism (e.g., *Sceloporus ochoterenae*; Smith et al., 2003).

Diet. — Diets were obtained for 45 lizards (for diet, see Table 1). Overall the Simpson's Index by prey item was 1.68. Mean number of prey items per stomach was 12.1 ± 2.24 ($N = 45$; range = 1–68). Body size had no effect on the number of prey items in a stomach ($N = 43$, $r^2 = 0.002$, $P = 0.78$). Males and females ate the same number of prey on average (Mann-Whitney U : $Z = -1.46$; $P = 0.14$). Mean volume of individual prey items in each stomach was 0.072 ± 0.014 cm³ ($N = 45$).

TABLE 1. Diet of *Sceloporus undulatus speari* from north-central Chihuahua, México.

Prey Taxon	Stomachs		Items		Volume (cm ³)	
	#	%	#	%	#	%
Invertebrates						
Arachnida						
Acari	2	4.44	2	0.28	0.0546	0.36
Aranea	4	8.89	5	0.71	0.2094	1.39
Insecta						
Coleoptera	35	77.78	119	16.90	4.9378	32.70
Diptera	8	17.78	12	1.70	0.8302	5.50
Hemiptera	10	22.22	15	2.10	0.3594	2.38
Heteroptera	1	2.22	1	0.14	0.12	0.79
Hymenoptera	29	64.44	531	75.30	5.4475	36.07
Lepidoptera	4	8.89	5	0.71	0.434	2.87
Megaloptera	2	4.44	3	0.43	0.240	1.59
Orthoptera	11	24.44	11	1.56	1.8425	12.20
Other						
Hatchling	1	2.22	1	0.14	0.464	3.07
<i>Uta stansburiana</i>						
Sand/Rock	1	2.22	–	–	0.032	0.21
Vegetation	2	4.44	–	–	0.131	0.87
Totals	45		705		15.1024	

Mean prey volume was unrelated to SVL ($N = 43$, $r^2 = 0.013$, $P = 0.55$). Males and females ate prey with similar mean volumes (Mann-Whitney U : $Z = -0.77$; $P = 0.44$).

The most prevalent prey items based on their occurrence in stomachs were coleopterans, which occurred in nearly 80% of stomachs, and in particular tenebrionids. Hymenoptera were also very common in stomachs, occurring in about 65% of stomachs, most of these were formicids. Numerically, hymenopterans, especially formicids, were by far the most important prey items, making up three-quarters of the diet. Coleopterans (again mostly tenebrionids) were numerically the second most important prey item. Volumetrically, hymenopterans and coleopterans were equally important, with each accounting for about a third of the volume of prey found in the stomachs. As in our population, coleopterans and hymenopterans are important components of *S. undulatus* diets throughout its range; however, the importance of each can vary significantly from population to population (e.g., Hamilton and Pollack, 1961; Jackson, 1973; Ferner, 1976; Ferguson and Bohlen, 1978; Ballinger et al., 1990; Parker, 1994).

One individual contained a hatchling *Uta stansburiana*. Parker (1994) found a juvenile *Scincella lateralis* in the stomach of a single individual of *S. u. hyacinthinus* in his study of a Mississippi population.

Conclusions. — The characteristics of the population of *Sceloporus undulatus speari* from the Transmontane sand dune region of northern Chihuahua that we studied fall within or close to the range of characteristics previously found for other populations and subspecies of *S. undulatus* throughout its range. It is interesting to note that some traits appear to vary among populations of *S. undulatus* more than others. For

example, diet and body temperature are remarkably similar, especially considering the geographic range encompassed by this species. However, traits such as clutch size, size at sexual maturity, and sexual dimorphism vary substantially, as does growth rate (see Niewiarowski and Roosenburg, 1993). Despite the fact that several populations of *S. undulatus* have been studied, we rarely have detailed information on several aspects of each population's ecology (e.g., we know a lot about a population's clutch size, but little on body temperature, perch use, or diet). We suggest that to fully understand the geographic variation within a wide-ranging species such as *S. undulatus*, we need more detailed studies on an array of key life history and other variables.

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