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Seasonal abundance, reproductive tactics and resource partitioning in two sympatric *Sceloporus* lizards (Squamata: Iguanidae) of México.

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Resumen: Se estudió a las lagartijas *Sceloporus grammicus* y *S. scalaris* en la Reserva de la Biosfera de La Michilía, México. Las necesidades y patrones de utilización de los recursos fueron similares en las dos especies, particularmente en su espectro de consumo de alimentos y en el patrón de su ciclos diarios de actividad. Las diferencias en elección de substrato no explican la coexistencia de esas dos abundantes especies; un desfase anual en su abundancia es una causa más probable, especialmente porque cada especie alcanza su abundancia máxima de adultos cuando los individuos adultos de la otra especie disminuye.

Key words: niche breadth, habitat selection reproductive patterns.

To the present, studies of resource partitioning have focused on the analysis of space utilization (Ortega *et al.* 1982), food acquisition (Barbault, *et al.* 1985) and temporal activity (Ortega *et al.* 1984), or their combined effect (Toft 1985). Efforts have been made to consider seasonal differences among potential competitive species and to evaluate the importance of such differences in explaining species coexistence. However, such studies in lizards are few (Ortega 1986).

The genus *Sceloporus* (Lacertilia: Iguanidae) has one of the broadest distributions in the American continent. It ranges widely throughout the Neartic from New England to Panama and inhabits also a large spectrum of habitats fluctuating from sea level to altitudes above 3500 m. *Sceloporus grammicus* Wiegmann is the third widest geographically distributed species of the genus.In the Mexican Republic it occurs in 25 states, and its distribution includes one state of the United States of America (Fig. 1). *S. grammicus* coexists with a very similar and related species, *S. scalaris* Wiegmann, with whom it shares a great part of its distributional range (Fig. 1). Both species of *Sceloporus* are very common in most of the places they inhabit.

The principal aim of this paper is to analyze the seasonal changes in niche structure and population density of two sympatric iguanid lizard populations, as well as to determine the causal factors for these differences.

La Michilía Biosphere Reserve is located in the State of Durango, México (104° 07' W - 104° 20' W; 23° 20' N - 23° 30' N) at an altitude between 2300 - 2800 m. It has a temperate climate with an average annual temperature ranging from 17.4 ° C to 20.7° C and receives from 525 to 609 mm of annual precipitation, strongly concentrated during summer (June to September). The predominant physiognomic-floristic unit of the area is oak-pine forest.

Population attributes and activity were studied as detailed by Ortega *et al.* (1984) and Ortega (1986).

The seasonal differences in insect abundance were also determined (Ortega 1986); areas adjacent to the study site were also systematically searched for active lizards and eleven kinds of microhabitat-substrates were recognized (Ortega *et al.* 1982).

Body characteristics, stomach contents and reproduction data were also recorded as explained in Ortega (1986).

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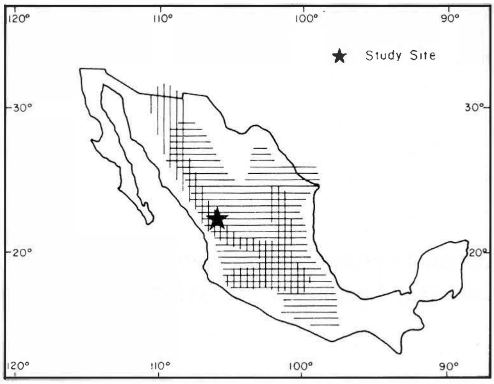

Fig. 1. Range of distribution of the Mexican lizards *Sceloporus grammicus* (horizontal lines) and *S. scalaris* (vertical lines).

Species differences of utilization of spatial, trophic and diurnal temporal resources were analyzed calculating niche breadth with Simpson's diversity index and niche overlap using Pianka's index (Pianka, 1973).

Sceloporus scalaris and *S. grammicus* are specialists in use of microhabitats utilization, but are generalists in their food habits and daily temporal activity (Table 1). *S. grammicus* is a fallen trunk dweller: most individuals were seen on fallen trees (59.6%) and fallen branches (15.0%). *S. scalaris* is a ground species (89.1%). Niche overlap along the microhabitat axis is very low, but high for food and activity over the day (Table 1).

In general, similarities of resource utilization are probably tied to the close resemblance of body features and thermal requirements (Table 2).

The differential use of substrates (divergent microhabitat specialization) helps to reduce competitive interactions between these species. If each species is active in a different microhabitat, both migth have access to different foods. However, this specialization is not necessarily, or even probably, induced by competition. Lizards strongly depend upon substrate adaptation to avoid predation, thermoregulate efficiently and defend territories successfully. Thus, it is not reasonable to explain divergent microhabitat specialization only on the basis of competitive pressures.

These species have high overlaps in food consumption and daily activity, which do not imply competition particularly because prey was not determined to species.

The same applies when overlap in daily activity is considered. The observed patterns are a result of generalized adaptations to ecological requirements, *i.e.* thermical adaptation, but are not the necessarily consequence of interspecific competition process.

Why do two sympatric species that hatch at the same size, grow at similar rates, eat basically the same food and are active during the same hours of the day, occur at such high and equal densities? Most of the age classes have high mortality rates (Table 3). Tail-loss, an indirect index of predation (Ortega, 1986), does not correspond with observed mortality rates (Table 3). Anyway, annual average population densities and biomass are high (Table 4), not only compared with the other lizard species of the guild (Ortega 1986), but also with the average density calculated for Sauria by Turner (1977).

Thus, neither competition nor predation explain the species successful coexistence. If we analyze the adult and subadult densities during a one year period (Fig. 2), it is possible to uncover another approach which bears on this question. The adults of *S. grammicus* reach high densities during September and October. During these months, the adults of *S. scalaris* are quite scarce. However, during October, the subadults of *S. scalaris* reach their highest number. During April and May, the adults of *S. scalaris* attain their highest abundance; while those of *S. grammicus* start declining, reaching their lowest values during June and July, when their juveniles reach their highest abundance. Maximum adult abundance of *S. scalaris* occurs when the adult abundance of *S. grammicus* is less than one half the density of *S. scalaris*. The inverse happens when adult individuals of *S. grammicus* reach their peak of abundance.

These complementary differences in abundance and an asynchronous population structure probably involve a reduction in competitive pressures between the closest age classes of both species (adults vs. adults, and subadults vs. subadults).

Differences in average annual age class abundances appear not to be mediated by competition, but rather by the distinct reproductive cycles of both species: *S. grammicus* is a viviparous "fall breeder" and *S. scalaris* is an oviparous "spring breeder" (Ortega 1986). In *S*.

TABLE 1

Diversity of substrate, food, daily temporal utilization by both Sceloporus *species, and niche overlap betwen them at La Michilía Reserve (n = sample size)*

Niche axis	Microhabitat	n	Trophic	n	Daily temporal	n
Niche breadth						
S. grammicus	0.15	(1,242)	0,31	(42)	0,68	(570)
S. scalaris	0,20	(408)	0,34	(38)	0,92	(417)
Niche overlap			Prey Taxa	Prey Size		
Both species	0.049		0,689	0.944	0.954	
(n)	(1,650)		(80)	(80)	(987)	

TABLE 2

Comparison of several features between S grammicus *and* S. scalaris *(n = sample size; the number between parenthesis is the standard errorr).*

Species	sex	Average new born size (mm)	n	Average new born weight (g)	n	Average growt rae (mm/day)	n	Average adult body size (mm)	n	Average adult jaw Length (mm)	n	Average adult cloacal Temp. (ºC)	n
S. grammicus	0	21.25 (0.721)	48	0,39 (0.015)	48	0064 (0.061)	49	53.97 (4.72)	208	6.42 (0.76)	208	30.54 (19.99)	38
	0	21.24 (0.834)	51	0.39 (0.013)	51	0.058 (0.048)	57	50.94 (5.54)	210	6.38 (0.40)	210	30.67 (10.02)	42
S. scalaris	0	20.38 (0.628)	62	0.38 (0.016)	62	0.060 (0.072)	74	51.24 (5.60)	207	7.06 (0.52)	207	31.16 (10.10)	55
	0	20.36 (0.621)	55	0.37 (0.016	55	0.062 (0.059)	67	52.53 (6.62)	205	7.15 (0.46	205	30.94 (9.69)	48

grammicus vitellogenesis, starts during mid or late August; ovulation begins in January (from early February to the first half of May all the females - even the smallest ones - exhibit oviducal eggs). Parturition occuring during the last half of May and maximum reproductive activity in males and females occurs during the same period (end of autumn).

For *S. scalaris* the reproductive activity along one year begins to be evident in April, when the first yolked follicles are observed (Ortega 1986). Ovulation takes place by the end of May, so that in June all females (even the smallest) exhibit oviductal eggs. This clutch is deposited by the end of June and is synchronized with a second yolk deposition period. In July all the females develop a second set of vitellogenic ovarian follicles. However, complete vitellogenesis and subsequent ovulation does not occur in all females. Thus, in August only 40% of the females carry oviductal eggs which are oviposited later in the same month. Maximum reproductive activity in males and females takes place during the spring.

Thus, differences in reproductive cycles cause the hatchlings of each species to be born during different seasons of the year, establishing this asynchronism and ultimately the complementarity of annual abundance.

Surely the reproductive cycles of each species have a strong genetic component resulting from phylogenetic constraints (each species belongs to a different *Sceloporus* species group), and also each reproductive cycle is admirably

TABLE 3

Age class mortality and percentage of individuals with tail loss for both populations (the number between parenthesis is the sample size; see text for explanation).

	S. grammicus		*S. scalaris*	
Age class	Mortality	Tail loss percentage	Mortality	Tail loss percentage
Embryos	0.071 (348)	-	0.272 (180)	-
Juveniles	0.696 (213)	1.1 (213)	0.755 (81)	9.1 (81)
Adults	1.000 (206)	47.13 (206)	1.000 (260)	44.65 (260)

TABLE 4

Density and biomass of both populations (the number between parenthesis is the standard error)

Species	Age Class	Average annual density /Ha	Average annual biomass /Ha
S. grammicus	Juvenile	124 (77)	112.84 (69.54)
	Adult	42 (12)	207.90 (59.14)
S. scalaris	Juvenile	165 (86)	151.90 (76.05(
	Adult	50 (13)	201.00 (64.54)

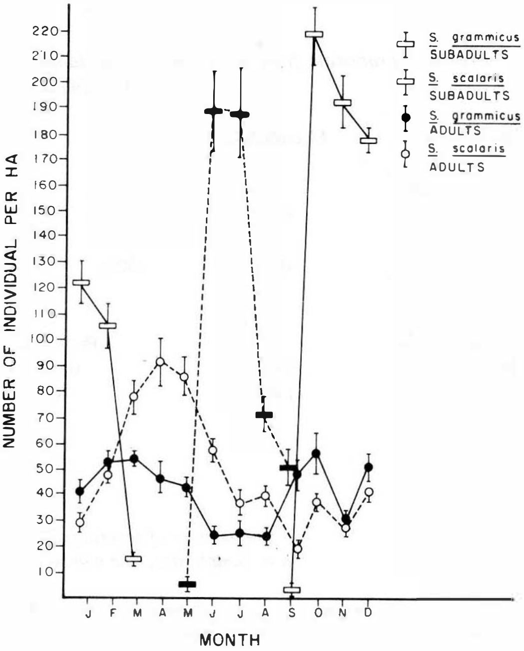

Fig. 2. Adult and subadult population densities for *S . grammicus* and *S. scalaris* for one year.

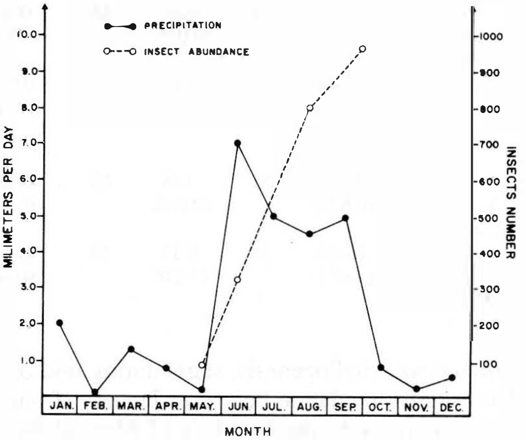

Fig. 3. Monthly precipitation mean and number of insects captured at La Michilia Biosphere Reserve during several months of 1981.

synchronized with the marked seasonality of the environment: hatchlings of *S. grammicus* are born just before the rainy season, when the abundance of the insect prey is highest (Figure 3). The hatchling can take advantage of this productive season for growing fast and reaching their sexual maturity in November. In contrast, female adult *S. scalaris* take advantage of the beginning of the rainy season to allocate more energy to the eggs of the first clutch and to allow a second clutch. Also, the eggs are oviposited when the soil is wet and when the best conditions for the incubation occur.

The complementary abundances of *S . grammicus* and *S. scalaris* seem not to be the result of competitive pressures. They are better understood as species-specific adaptations to their environment, mainly to the marked seasonal changes of climatic factors and to prey availability in this temperate forest. Ecological adaptations are also consequences of the striking differences in reproductive modes exhibited by the two species. However, this annual displacement of densities could be a factor contributing (as a side effect) to lowered interspecific competition.

Much work remains to be done to elucidate the influence of predation pressure on possible competitive interactions between *S. grammicus* and *S. scalaris,* to study other populations of these same species along their wide ranges of distribution and to test these hypotheses in other taxa. However, for *S. grammicus* and *S. scalaris* populations at La Michilía, the annual abundance complementarity joined with distinct substrate preferences, seem to be the key to their coexistence.

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