species specificity of sexual pheromone trails appears to evolve rapidly when selection pressure for reproductive isolation is present; second, in *Thamnophis marcianus*, trail pheromones are primarily involved in reproductive activity.

Acknowledgments.—This project was conducted with support from a University of Texas at Tyler faculty research grant to NBF. Support during preparation of the manuscript was given by the Department of Energy contract DE-AC09-76SR00819 to the University of Georgia Institute of Ecology (SREL). We thank J. Ford, W. Lamar, W. Cooper, R. Seigel, J. Knight and S. Novak for critically reviewing the manuscript.

## LITERATURE CITED

- BROWN, W. S., AND F. M. MACLEAN. 1983. Conspecific scent trailing by new born timber rattlesnakes, *Crotalus horridus*. Herpetologica 39: 430-436.
- BURGHARDT, G. M. 1970. Chemical perception in reptiles. In J. Johnson, D. Moulton and A. Turk (eds.), Advances in Chemoreception. Pp. 241– 308. Appleton Century Crofts, New York.
- DEVINE, M. 1977. Chemistry and source of sexattractant pheromones and their role in mate discrimination by garter snakes. Ph.D. Dissertation. Univ. Michigan, Ann Arbor. 73 pp.
- DUNDEE, H. A., AND M. C. MILLER, III. 1968. Aggregative behavior and habitat conditioning by the prairie ringneck snake, *Diadophis punctatus arnyi*. Tulane Stud. Zool. Bot. 15:41-58.
- FORD, N. B. 1979. Aspects of pheromone trailing in garter snakes (*Thamnophis*). Ph.D. Dissertation. Miami Univ., Oxford, Ohio. 85 pp.
- ——. 1981. Seasonality of pheromone trailing behavior in two species of gartersnake, *Tham-nophis* (Colubridae). Southwest. Nat. 26:385– 388.
- ——. 1982. Species specificity of sex pheromone trails of sympatric and allopatric garter snakes (*Thamnophis*). Copeia 1982:10-13.
- —, AND C. W. SCHOFIELD. 1984. Species specificity of sex pheromone trails in the plains garter snake, *Thamnophis radix*. Herpetologica 40:51-55.
- ——. 1986. The role of pheromone trails in the sociobiology of snakes. In D. Duvall, D. Muller-Schwarze, and R. Silverstein (eds.), Chemical Signals in Vertebrates, IV. Plenum Press, New York.
- FOUQUETTE, M. J., JR. 1954. Food competition among four sympatric species of garter snakes, genus *Thamnophis*. Texas J. Sci. 6:172–188.
- GEHLBACH, F. R., J. F. WATKINS, AND J. C. KROLL. 1971. Pheromone trail-following studies of typhlopid, leptotyphlopid, and colubrid snakes. Behaviour 40:282–294.
- GREGORY, P. T. 1975. Aggregation of gravid snakes in Manitoba, Canada. Copeia 1975:185-186.
- KARGES, J. P. 1983. Reproductive biology and

seasonal activity of the checkered gartersnake (*Thamnophis marcianus*). M.S. Thesis. Univ. Texas at Arlington. 224 pp.

- MILSTEAD, W. W. 1953. Geographic variation in the garter snake, *Thamnophis cyrtopsis*. Texas J. Sci. 5:348–379.
- RAUCH, J. 1978. Integumentary bloodvascular system in garter snakes *Thamnophis sirtalis parietalis* and *T. radix*). Can. J. Zool. 56:469–476.
- RUTHVEN, A. G. 1908. Variations and genetic relationships of the garter snakes. Bull. U.S. Natl. Mus. 61:1-201.
- SIEGEL, S. 1956. Nonparametric Statistics for the Behavioral Sciences, McGraw-Hill, New York. 312 pp.
- TENNANT, A. 1984. The Snakes of Texas. Texas Monthly Press. Austin. 561 pp.
- WEBB, R. G. 1980. Thamnophis cyrtopsis. In Cat. Amer. Amphib. Rept.:245.1-245.4.

Accepted: 8 July 1985.

Journal of Herpetology, Vol. 20, No. 2, pp. 262-264, 1986 Copyright 1986 Society for the Study of Amphibians and Reptiles

## Herbivory in a Small Iguanid Lizard, Sceloporus torquatus torquatus

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Since the work of Szarski (1962), many authors have discussed the ingestion of plant material by lizards (e.g., Pough, 1973; Iverson, 1982) reporting new data and proposing new hypotheses. In general, these works have dealt with large lizards (Sauromalus, Iguana, Dipsosaurus, etc.) and little attention has been paid to small omnivorous lizards. To achieve a synthetic view of omnivory and herbivory, it is important to document more cases of herbivory-omnivory and analyze the growing list of so-called "atypical" small lizards that include plant structures in their diet. Here we document the omnivorous summer diet of a population of the relatively small lizard Sceloporus torquatus torquatus Wiegmann (adult mass = 11-43 g; adult snout-vent length = 70-100 mm) and add information on sexual dimorphism.

The natural history of Sceloporus torquatus torquatus has been described by Smith (1936) and

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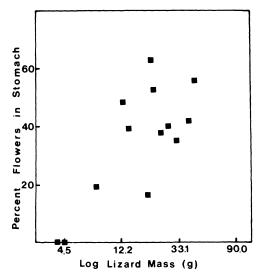


FIG. 1. Percentage of stomach content (dry weight) attributable to flowers as a function of body mass in *Sceloporus t. torquatus* collected in July 1984. y = 18.3 (ln mass -18.4; product-moment correlation r = 0.74; N = 13; t = 3.65; P < 0.005).

Duellman (1961), and the age structure and sexual size differences of some populations have been worked out by Davies and Smith (1953) and Fitch (1978). In a population in Querétaro, México, Staton and Conzelmann (1975) found an almost purely insectivorous diet and a rare case of cannibalism. Although Pough (1973) suggested that iguanid lizards weighing less than 100 g were almost completely carnivorous, it has long been known that some relatively small sceloporine lizards are partial leaf, fruit and flower eaters (S. magister: Taylor, 1938; S. poinsetti, S. clarki and S. orcutti: Stebbins, 1954; S. mucronatus: Méndez and Villagrán, 1983). Ingestion of buds and flowers of wild scarlet runner bean (Phaseolus coccineus) by Sceloporus torquatus was documented by Búrquez (1979) and Búrquez and Sarukhán (1980).

The study site was located in the Volcanic Axis on the southern limit of the Mesa Central in the Chichinautzin range (3000 m), near Km 41.5 on the Mexico-Cuernavaca federal highway. The topography of the area is heterogeneous, comprising low volcanic hills composed mainly of Quaternary basaltic blocks and lava. Coniferous forest (Pinus rudis and Abies religiosa) dominates with many species of grasses present in the understory and open areas (Burquez, 1979). Lizards were captured by hand during July and August 1984. Stomach contents, mass, and sexual size difference data were recorded for 29 lizards humanely killed (13 "early season," July 1984 and 16 "late season," August 1984). Another 39 individuals were sexed and measured, then released. Stomach

TABLE 1. Snout-vent length and mass of Sceloporus t. torquatus ( $\bar{x} = \text{mean}$ , R = range, N in parentheses). Superscript indicates mean values that are not significantly different (Wilcoxon twosample test; P > 0.05).

|                |   | SVL (mm)               | Mass (g)  |
|----------------|---|------------------------|-----------|
| Adult ð        | x | 90.2 (12) <sup>a</sup> | 32.1 (10) |
|                | R | 81.2-97.4              | 23.5-43.0 |
| Adult <b>♀</b> | x | 80.3 (13)ª             | 21.4 (10) |
|                | R | 71.5-91.4              | 11.8-34.0 |
| Juvenile       | x | 55.5 (14)              | 8.9 (9)   |
|                | R | 40.0-74.3              | 3.3-19.0  |

contents were obtained through dissection. Contents were fractioned and the dry weight of each fraction was obtained after drying the samples in an oven at 80°C for 24 h.

Stomachs contained diverse arthropods, the most common being insects. During the summer, there was a shift in the relative proportions of ingested material, with plant material, mainly flowers of P. coccineus becoming more important, especially in adult specimens. The floral fraction contained in lizard stomachs was correlated with lizard body mass (Fig. 1, r = 0.74, N = 13, P < 0.005). Apparently, the ingestion of floral material begins early in life and becomes more important as size increases (Fig. 1). Later in the season the components of the diet shifted again to a predominantly insectivorous pattern: five adult specimens taken after the flowering peak in late August contained almost no plant material (percentage plant material in stomach, early season = 42.4, N = 8; late season = 3.8, N = 5). During this time the flowers were less abundant, the plants were taller, and the flowers might have been out of the reach of the lizards. A large fraction of the dry weight stomach content was composed mainly of medium to large sized insects (Lepidoptera 34.2%, Coleoptera 19.2%, Hymenoptera [Formicidae] 17.7%, other arthropods, 26%, comprising almost equal proportions of Homoptera, Dermaptera, Diptera, Hemiptera, Aranae and Acarinae).

No sexual size dimorphism is apparent when snout-vent length is considered (Wilcoxon twosample test,  $U_s = 91$ , P > 0.05); these data support the conclusion of Fitch (1978). However, significant differences between sexes appear when body mass is compared (Wilcoxon two-sample test,  $U_s =$ 115, P = 0.05). Males by their larger body mass are expected to consume more flowers, but due to the small sample size no firm conclusions can be drawn about sex differences in diet. Interestingly, there are no reports of ontogenetic changes of diet in this genus as has been reported for different Iguaninae (e.g., Van Devender, 1982 and citations in Iverson, 1982). Our results show the dependence of herbivory on body mass at the intraspecific level, but do not support the idea of body mass as the main determinant of herbivory. As shown before, many small lizards have partially or totally herbivorous diets. Other adaptations can lead to a herbivorous existence (i.e., colic modifications and symbionts, see Iverson, 1982). We suggest that *S. t. torquatus* uses flowers opportunistically. Subjective observations of the relative abundance of insects reveal that many of the species found in the late collected lizards were scarce at the beginning of the season. Thus, plants were exploited when insects were in short supply and the flowers themselves were abundant (see Pike et al., 1977).

Some sceloporine lizards with an adult snoutvent length of more than 70 mm, but weighing less than 100 g can be classified as dietarily opportunistic (see Taylor, 1938 and Stebbins, 1954) but others cannot be strictly viewed as opportunistic. Some small iguanids, although classified as opportunistic, rely heavily on plants. Sceloporus mucronatus mucronatus eats as much as 75% plant material during December and always include some plants in its diet (Mendez and Villagran, 1983). The cavernicolous xantusid Lepidophyma smithii can survive in captivity with an almost pure plant diet (Mautz and Lopez-Forment, 1978), and some small iguanid species studied in the Bahamas by Schoener et al. (1982), include in their diet a fairly large proportion of plant material. Although the availability of plant material was not measured in these studies, it is possible that lizards were using plants in a fine grained manner. In other words, plant items are taken in proportion to their abundance through time. If this pattern occurs, the notion of obligate or opportunistic plant-eaters surely will change.

Acknowledgments.—R. Dirzo and R. C. Vogt made helpful comments on an earlier draft of the manuscript. H. Drummond suggested changes and rearrangements; his comments and encouragement are greatly appreciated.

## LITERATURE CITED

- BÚRQUEZ, A. 1979. Biología floral de poblaciones silvestres y cultivadas de *Phaseolus coccineus* L. Tesis de licenciatura. Facultad de Ciencias, Universidad Nacional Autónoma de México. México, D.F.
- , AND J. SARUKHAN. 1980. Biología floral de poblaciones silvestres y cultivadas de *Pha*seolus coccineus L. I. Relaciones planta-polinizador. Bol. Soc. Bot. Mex. 39:5-24.
- DAVIES, J., AND H. M. SMITH. 1953. Lizards and turtles of the Mexican State of Morelos. Herpetologica 9:100-108.

- DUELLMAN, W. E. 1961. The amphibians and reptiles of Michoacan, Mexico. University of Kansas Publ. Mus. Nat. Hist. 15:1-148.
- FITCH, H. 1978. Sexual size differences in the genus Sceloporus. University of Kansas Science Bull. 51:441-461.
- IVERSON, J. B. 1982. Adaptations to herbivory in iguanine lizards. *In* Burghardt, G. M. and S. Rand (eds.), Iguanas of the World, Their Behavior, Ecology and Conservation. Pp. 60–76. Noyes Publ. Park Ridge, N.J.
- MAUTZ, W. J., AND W. LOPEZ-FORMENT. 1978. Observations on the activity and diet of the cavernicolous lizard *Lepidophyma smithii* (Sauria: Xantusiidae). Herpetologica 34:311–313.
- MÉNDEZ, F. R., AND M. VILLAGRÁN. 1983. Contribución al conocimiento de la ecología y ciclo reproductor de la lagartija vivipara Sceloporus mucronatus mucronatus. Tesis de licenciatura. Escuela Nacional de Estudios Profesionales Iztacala. México, D.F.
- PIKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of the theory and tests. Quart. Rev. Biol. 52:137– 154.
- POUGH, F. H. 1973. Lizard energetics and diet. Ecology 54:837-854.
- SCHOENER, T. W., J. B. SLADE, AND C. H. STINSON. 1982. Diet and sexual dimorphism in the very catholic lizard genus, *Leiocephalus* of the Bahamas. Oecologia (Berl.) 53:160–169.
- SMITH, H. M. 1936. The lizards of the torquatus group of the genus Sceloporus Wiegmann 1828. University of Kansas Science Bull. 24:539-543.
- STATON, M. A., AND J. CONZELMANN. 1975. Cannibalism in Sceloporus torquatus torquatus Wiegmann (Reptilia: Sauria). Southwest. Nat. 20: 147-148.
- STEBBINS, R. C. 1954. Amphibians and Reptiles of Western North America. McGraw-Hill. New York.
- SZARSKI, H. 1962. Some remarks on herbivorous lizards. Evolution 16:529.
- TAYLOR, H. 1938. Notes on the herpetological fauna of the Mexican State of Sonora. University of Kansas Science Bull. 24:475-503.
- VAN DEVENDER, R. W. 1982. Growth and ecology of the spiny tailed and green iguanas in Costa Rica, with comments on the evolution of herbivory and large body size. *In* Burghardt, G. M. and S. Rand (eds.), Iguanas of the World, Their Behavior, Ecology and Conservation. Pp. 162–183. Noyes Publ. Park Ridge, N.J.

Accepted: 19 July 1985.