THERMOREGULATION AND ECCRITIC BODY TEMPERATURES IN MEXICAN LIZARDS OF THE GENUS **SCELOPORUS**

By CHARLES M. BOGERT.
The American Museum of Natural History. New York, N. Y., U. S. A.

INTRODUCTION

Lizards of the genus **Sceloporus** occur in a variety of habitats in North America between the latitudes of 8° and 42° N. Smith (1946) recognizes 102 species and subspecies, the majority of them occurring in Mexico, where they range from near sea-level in the most humid portions of Veracruz to elevations at least as high as 4500 meters. Other species prefer moderately flat or sparsely wooded terrain in the more arid portions of Mexico, where they may be restricted to canyon walls, or to trees along rivers. In Honduras one species is largely confined to cleared areas in cloud forests. Not only are lizards of the genus widespread, but they are among the more abundant diurnal reptiles ordinarily encountered in the field. Hence the various species of **Sceloporus** are better suited than many other lizards for ecological studies, more especially since Smith (1939 and **supra cit.)** has mapped the ranges of the species, and provided a reasonably stable nomenclature.

Thermoregulation in reptiles has been the subject of few investigations, although several have dealt with thermal tolerances, and particularly with lethal temperatures at the upper end of the scale. Techniques used have been described by Herter (1940), by Cole (1943), by Cowles and Bogert (1944), who define the critical thermal levels, and by Colbert, Cowles, and Bogert (1946). Various aspects of the problem of thermoregulation in reptiles, based largely upon

work carried on in the United States, are discussed by Bogert (1949). However, a solution to many problems can be obtained only by extending the scope of investigations to include data for comparison from several regions.

In a previous paper (Bogert, **supra cit.**) it has been shown that diurnal lizards of the genera **Sceloporus** (Iguanidae) and **Cnemidophorus** (Teiidae) occur side by side in almost identical habitats, and yet maintain significantly different thermal levels of the body. Often the difference between the means of normal activity ranges of lizards in these two genera approximates 6° C. On the other hand, two species of **Sceloporus** from such ecologically divergent regions as Florida and Arizona maintain thermal levels of the body that are virtually identical, with no statistically significant difference between means (Bogert, **supra cit.**).

The purpose of the present paper, therefore, is to compare the preferred or "eccritic" body temperatures of several species of **Sceloporus** in order to demonstrate that closely related species tend to have similar preferences, and to maintain similar thermal levels in the body under divers ecological conditions, in the deserts, mountains, foothills, and valleys of temperate, subtropical, and tropical portions of North America.

METHODS

All data were secured under field conditions from lizards killed with a pistol, using .22 "dust shot" ammunition as described in greater detail by Bogert **(supra cit.)**. Body temperatures, accurate to within .2° C., were taken immediately after each lizard was shot. A special thermometer was used, so designed that it came to equilibrium within approximately 15 seconds after being thrust into the lizard's cloaca. Air temperatures were taken at 2 to 5 cm. above the place where the lizard was first observed, or to one side in the case of lizards on fence posts or tree trunks. It is difficult, and sometimes impossible with portable apparatus, to obtain reliable measurements of the temperature of solid objects, such as rocks, logs, or trees, where some **Sceloporus** are more commonly encountered. At best substratum records are little more than approximations, and probably represent lower mean values than actually existed.

It is assumed that, by assembling data for series of lizards under normal, active, conditions, a reliable index to the body temperature

variations or the "normal activity range" (Cowles and Bogert, **supra cit.)** of any given population can be obtained. This zone of preference, readily expressed quantitatively in terms of the mean and extremes of the sample, can therefore be compared for different populations. It has been shown previously (Bogert, **supra cit.)** that under normal field conditions the diurnal lizards thus far studied are able to maintain the body temperature within rather definite limits by means of behavioral thermoregulation (principally by basking to raise the level, or by seeking shelter, to lower it), and that the eccritic or preferred body temperature is not dependent upon size, sex, or season. It follows, therefore, that the sexes need not be considered separately, and that data concerning body volume or season need not be included in the tabulations below. Most of the data presented were secured in Mexico, but some obtained in the United States and Honduras are included in order to offer more extensive comparisons.

RESULTS AND DISCUSSION

The data obtained by the methods described above are summarized in Table 1, wherein information concerning the latitude and elevation have been added. The mean of the normal activity range is indicated, with the extremes given below in parentheses. As originally defined by Cowles and Bogert **(supra cit.,** p. 277), the normal activity range "is the thermal range [of the body] extending from the resumption of ordinary routine (after the animal has ceased basking, in the case of diurnal forms) and terminating at a point just below the level at which high temperatures drive the animal to shelter".

This definition was based upon observations of animals kept in cages set up in the field, under conditions where individual lizards could be watched throughout the day. Under the conditions employed when data were being secured for this study it was impossible, of course, to know anything of the activities of individual lizards prior to the time when they were first observed and shot. The majority of those taken in the field obviously had already raised body temperatures to the threshold of the normal activity range. However, it is apparent that a few lizards are abroad, occasionally before sunrise but sometimes even later, that have not yet reached this threshold. Fortunately it is a relatively easy matter to separate such low records,

Species	Locality	Elevation in Meters	Approximate Latitude N. of Equator	Air Temperature, Mean, ° C.	Substratum Temperature, Mean, ° C.	No of Observations	Body Temperature, Mean, ° C.	Coefficient of Variation
S. m. magister	Superior, Arizona	1200	33°	32.5	32.6	10	34.9±.56 (32.0 to 37.2)	5.7
S. u. consobrinus	Chihuahua, Chihuahua	1400	28°	26.6	32.3	44	34.8±.23 (31.8 to 38.9)	4.4
S. woodi	Hicoria, Florida	60	27°	——	——	42	36.2±.25 (32.0 to 39.2)	4.5
S. merriami	Las Delicias, Coahuila	1500	25°	32.6	32.8	11	33.6±.76 (29.6 to 37.4)	7.4
S. poinsettii	La Goma, Durango	1100	25°	28.6	31.8	19	34.2±.41 (31.4 to 38.4)	5.3
S. g. disparilis	La Goma, Durango	1100	25°	27.2	42.5	38	33.6±.30 (30.3 to 39.1)	5.6
S. v. variabilis	Palictla, San Luis Potosí	150	21°	29.5	——	38	36.9±.24 (33.6 to 40.0)	4.1
S. v. olloporus	El Zamorano, Honduras	800	14°	27.6	36.6	72	35.4±.15 (33.1 to 38.8)	3.7
S. squamosus	El Zamorano Honduras	800	14°	30.8	40.2	13	35.3±.52 (32.5 to 38.0)	5.2
S. f. malachiticus	Honduras and San Juancito, Cerro Uyuca,	1500 to 2200	14°	19.1	24.2	22	32.9±.38 (30.0 to 35.8)	5.5

TABLE 1. Summary of pertinent geographical and ecological data for samples of representative species and subspecies of lizards of the genus **Sceloporus.** Extremes for the "normal activity range" in body temperature of each sample are given in parentheses below the mean and its standard error. Body temperatures were obtained with a thermometer thrust into the lizard's cloaca immediately after it had been shot. Substratum temperatures were recorded at the exact spot where individual lizards were first seen, and air temperatures were taken 2 to 5 cm. above or to one side of the same spot.

assumed to be in the "basking range," from those in the normal activity range when the raw data are plotted in a simple histogram (Fig. 1) showing the frequency distribution of individual body temperatures (plotted by degrees on the Centigrade scale, without reference to fractions of degrees in the original data). It is manifest from this method of analysis that few lizards are abroad before the threshold of the normal activity range is reached. When samples are sufficiently large there is a sharp line of demarcation between this range, which approximates a normal curve, and the basking range. Observations, both in the field as well as in laboratory cages provided with heat lamps, suggest that most lizards bask in secluded places, sometimes with only the head above the sand, before they venture into the open to assume their routine activities. This readily accounts for the few records included within the basking range.

Habitats.—Basking is characteristic of all lizards in the genus **Sceloporus,** and there are many indications that the genus is not represented in some areas largely because there are too few days during the year when direct sunlight is available (Bogert, **supra cit.).** But in warmer regions, or more especially in regions of intense summer heat, lizards must seek shelter to avoid reaching body temperatures much beyond the upper limit of the normal activity range.

The habitats occupied by individual species reflect their needs for basking as well as for shelter. Five of the ten species listed in Table 1 occupy arid regions in the Sonoran and Chihuahuan deserts (as mapped by Shreve, 1942) or around their borders, yet the habitat of each provides some means of avoiding excessively high temperatures. **Sceloporus m. magister** inhabits rocky areas in canyons or foothills, or in flat desert situations where plants such as the mesquite **(Prosopis chilensis)** or the Joshua tree **(Yucca brevifolia)** attain the size of trees; this lizard is unlikely to be found in regions where such shrubs as the creosote bush **(Larrea divaricata)** provide only scanty shade. Two of the species, **S. merriami,** and **S. poinsettii** are restricted to rocky areas or cliffs where crevices provide cool retreats from direct sun. **S. undulatus consobrinus,** essentially a plains element that penetrates the Chihuahuan desert, was found only in places where small rock piles or sufficiently dense shrubs or trees provided some sort of shelter. The fifth, **S. grammicus disparilis,** is seemingly less restricted elsewhere, but at La Goma in Durango where the thermal data were secured, it was confined to the trunks or stumps of the large willow **(Salix)** and cottonwood **(Populus)** trees growing along the Rio Nazas.

Terrestrial situations at the same locality were occupied by three other species of the same genus.

In peninsular Florida **S. woodi** is largely confined to areas designated as rosemary scrub, and at the Archbold Biological Station the species was most abundant along roads or fire lanes where it could bask in the open. At Palictla in the lowlands of San Luis Potosí **S. variabilis variabilis** inhabits a densely forested region (included in the "Bosque Tropical" by Arias, 1942), although it was not seen except in clearings or along roads. In the Yeguare River Valley of Honduras, **variabilis** is represented by another subspecies, **olloporus,** that shuns the **ocotal** or pine forest at the edges of the valley and lives in the xerophytic scrub or along streams and arroyos in the warm lowlands. **S. squamosus** differs but litle from **S. v. olloporus** in habitat, but manifests a greater preference for isolated rocks in open situations.

S. formosus malachiticus, in the same general region as **squamosus** and **olloporus,** is ecologically isolated from both. It occurs principally above 1500 meters, where it is essentially a cloud forest form, although it is encountered at slightly lower elevations than true cloud forest. Despite its preference for humid, densely wooded, mountains, it avoides the dense forests themselves, and lives in clearings where it is most often seen basking on fences, logs, stumps, or the tile roofs of human habitations.

In other words, to summarize these comments concerning habitats, when lizards of the genus **Sceloporus** live in arid regions, they are restricted to terrain where shelter from the sun is available, whereas when they are found in densely forested areas, they occur only in situations where they have ready access to direct solar radiation. Thus, behavioral control is dependent upon the selection of habitats wherein the lizard can regulate the absorption as well as the dissipation of body heat by means of movement within limited space. Moreover, as pointed out by Cowles and Bogert **(supra cit.)** the orientation of the body with respect to the sun's rays may be modified so as to receive the maximum amount of heat when the body temperature is low, or so as to receive a minimum when the body temperature is high, as a further refinement of basking.

Cycles of activity.—It is difficult to make generalizations concerning daily or seasonal cycles of activity among lizards of the genus **Sceloporus.** In hot, arid, regions they are more often abroad during the early morning hours, but seek shelter when the sun reaches its zenith. They may re-emerge, usually in smaller numbers, in the late

afternoon or during the twilight hours, although their activities are dependent upon local weather conditions. In the Yęguare River Valley of Honduras virtually no **Sceloporus** could be collected on days when the sky was overcast. Similarly, **S. f. malachiticus** in the cloud forests could be found abroad only on clear days rarely before 12 M., and often not until late in the afternoon, at the time of day when desert lizards would have retreated to shelter.

In temperate zones, of course, no lizard is active throughout the year. Seasonal cycles of activity presumably are the result of changes in the thermal level of the environment, not merely of lower air and substratum temperatures during the winter, but of the more direct effect of there being fewer hours of sunlight available for basking. In the tropical portions of North America **Sceloporus** is active throughout the year. It is perhaps significant that the species with the lowest mean temperature (Table 1) for its normal activity range is **S. f. malachiticus** of the tropical cloud forests, where environmental temperatures are prevailingly low, but where occasional basking is possible throughout the year.

Little is known of the sex cycle of lizards in the genus, although the data available indicate that most species in temperate zones deposit their eggs in late spring or in early summer (June and July, Stebbins, 1944; May to July, Woodbury and Woodbury, 1945) regardless of the rainy season, whereas in the tropics oviposition is keyed to the dry season. Smith (1939) makes the pertinent observation that in Mexico all species occurring above 10,000 feet elevation belong to one of three ovoviviparous groups, whereas oviparous species gradually replace the ovoviviparous species until at 1000 feet or lower only a few ovoviviparous species occur. He attempts no explanation although it appears to be a reasonable inference that retention of the eggs within the body of the female enables her to maintain them at suitable high thermal levels by basking in regions where mean temperatures of the subsoil are below normal incubation temperatures. Significantly, well developed embryos were found in **S. f. malachiticus** taken early in February at 1800 meters on Cerro Uyuca in Honduras. This was shortly after the onset of the dry season when clear days in cloud forests occur with greater frequency than during other seasons. In contrast, **Sceloporus c. clarki** in Arizona is reported by Kauffeld (1943) to contain eggs with developing embryos during the month of August.

Unfortunately there are precise data concerning the breeding habits of so few species of **Sceloporus** that little more can be said

with reference to cycles of activity and thermoregulation. However, it is manifest that there are interrelationships between cycles of activity and thermoregulation, as well as the breeding cycle.

CONCLUSIONS

Even though it is often stated in texts that "reptiles have the temperature of the surrounding atmosphere", it has been shown that this is a half-truth at best largely derived from observations of reptiles under captive conditions. Herter (1940) attempts to demonstrate that correlations exist between the preferred mean substratum temperatures and the altitudinal and latitudinal distributions of the species that he tested in the laboratory. However, as explained previously (Bogert, **supra cit.**), Herter's ignorance of the body temperatures of the reptiles tested leaves most of his conclusions open to criticism and doubt. Nonetheless his work reflects the ability of reptiles to discriminate between thermal levels and to react in a positive manner to gradients in the temperature of the substratum.

The data presented in Table 1 show that there is no correlation between preferred body temperature levels and altitudinal or latitudinal distributions. The extremes of the normal activity ranges of ten species of a single genus are remarkably close as may be seen in Figure 2 where the thermal ranges of five population samples are shown graphically. Even though all samples are not adequate, it is evident that lizards of the genus **Sceloporus** can exist in diversified habitats, and still maintain the thermal level of the body within the range of 29.6° and 40.0° C. Differences between the means of the normal activity ranges do not exceed 4° C. for populations between a latitudinal range of 19° encompassing approximately 1000 miles, and representing at least five of the climatic provinces mapped by Thornthwaite (1931).

It should be understood, of course, that geographical regions having certain temperature characteristics, as depicted by Thornthwaite, deal with broad climatic conditions and do not attempt to describe local variations. Nonetheless, it is plain that the mean body temperature of such heliothermic lizards as the ten species of **Sceloporus** studied, is not closely correlated with either mean air or substratum temperatures. In fact the eccritic body temperature of **S. f. malachiticus** is 23.8° C. higher than the mean air temperature, and 18.7° C. higher than the mean substratum temperature in its

cloud forest habitat. Similarities between eccritic temperatures of the several species can be ascribed to (a) habitat selection and to (b) behavioral thermoregulation. These are quite probably correlated with adaptive modifications in adult size, body proportions, skin texture, and other characters less readily perceived, as suggested by Bogert (1949).

SUMMARY

Ten species and subspecies of the iguanid genus **Sceloporus** were studied under field conditions in the United States, Mexico, and Honduras, between the latitudes of 14° and 33° in North America, and at elevations varying from 60 meters to 2200 meters. Means for the normal activity ranges, or eccritic body temperatures, of the ten varied from only 32.9° C. for a cloud forest species in Honduras, to 36.9° for a species in the tropical lowlands of San Luis Potosí. When abroad and active the majority of these heliothermic lizards maintain the body temperature within extremes scarcely more than 4° C. above or below a mean that approximates 34° to 35° C. Although there are slight differences between species, the lizards of the genus evidently maintain body temperatures within a zone of preference ranging from 29.6° to 40.0° C. Eccritic body temperatures are not closely correlated with those of the air or substratum, nor with altitude or latitude. The maintenance of relatively constant body temperatures is primarily a reflection of the lizard's ability to regulate the absorption of solar heat by means of its behavior, although habitat selection, probably coupled with adaptive modifications in the morphology and in the breeding cycle of individual populations, permits each species to maintain a thermal level that is more or less characteristic of its genus.

ACKNOWLEDGMENTS

For numerous favors in connection with the assemblage of the data used in this report the writer is indebted to the following individuals: Señor Pedro Moreno of Samalayuca, Chihuahua; Mr. Frank Fry, Superintendent of the Babícora Development Company, Babícora, Chihuahua; Mr. Fred Gibson of the Boyce Thompson Southwestern Arboretum at Superior, Arizona; Mr. Richard Archbold of the Arch-

bold Biological Station at Lake Placid, Florida; the Presidente del Comisariado Ejidal at Palictla, San Luis Potosí; Dr. A. F. Carr, Jr., of the Escuela Agrícola Panamericana at El Zamorano, Honduras; and the numerous officials of the Mexican Government whose treatment was unfailingly courteous throughout the Republic.

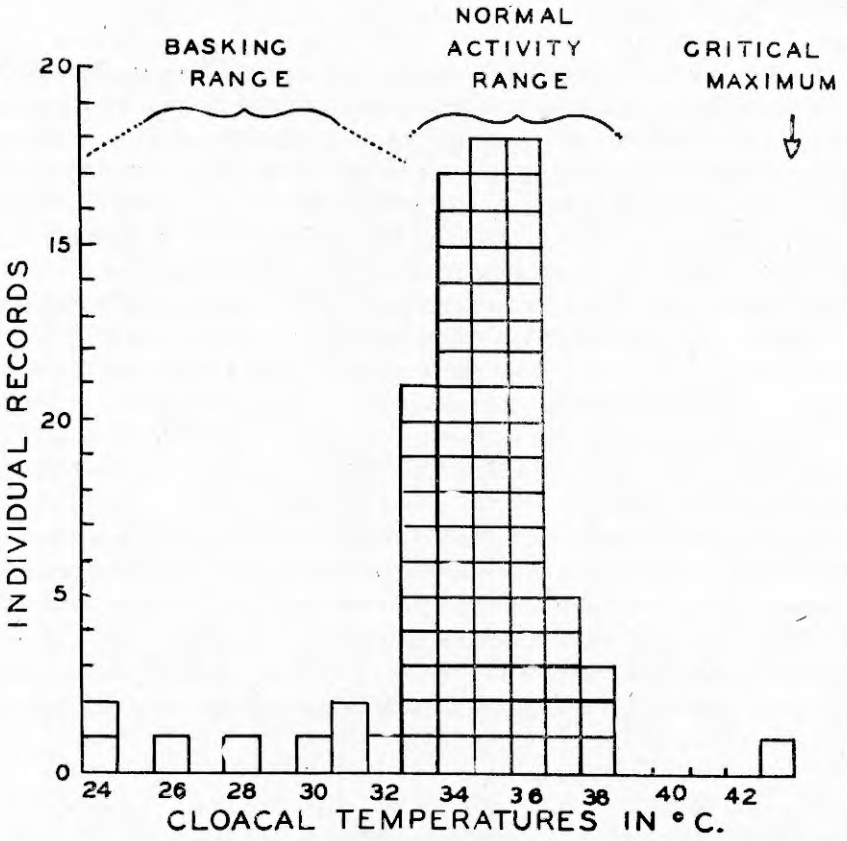

Fig. 1.—Histogram, with cloacal temperatures for individual lizards **(Sceloporus variabilis olloporus)**, secured under field conditions in Honduras, plotted to show the method used in ascertaining the limits of the normal activity range. Each square represents the temperature of a single lizard, plotted with fractions above even degrees ignored. A single record for the critical maximum (or "the thermal point at which locomotor activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death" as defined by Cowles and Bogert, 1944) is included. This was obtained by exposing an adult male to direct solar radiation for a period of ten minutes. Prolonged exposure to temperatures between the upper level of the normal activity range and the critical maximum also result in death

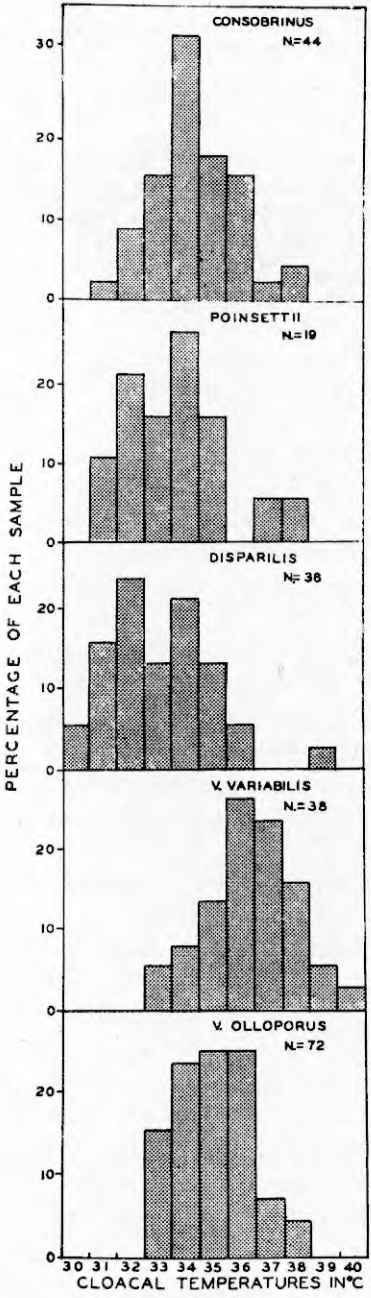

Fig. 2. Histograms showing the distribution of cloacal (body) temperatures in representative samples of five populations of lizards of the genus **Sceloporus: S. undulatus consobrinus, S. poinsettii, S. grammicus, S. v. variabilis,** and **S. variabilis olloporus.** Cloacal or body temperatures (secured under field conditions at the localities indicated in Table 1) are plotted as in Fig. 1, but to facilitate comparisons each sample is shown on a percentage basis.

LITERATURE CITED

ARIAS, ALFONSO CONTRERAS, 1942.—Mapa de las provincias climatológicas de la república Mexicana. Inst. Geogr., México, xxv+54 pp., figs. 1-4, 2 maps.

BOGERT, CHARLES M., 1949.—Thermoregulation in reptiles, a factor in evolution. Evolution, Vol. 3, pp. 195-211, 3 figs.

COLBERT, EDWIN H., RAYMOND B. COWLES, and CHARLES M. BOGERT, 1946.—Temperature tolerances in the American alligator and their bearing on the habits, evolution and extinction of the dinosaurs. Bull. Amer. Mus. Nat. Hist., Vol. 86, pp. 327-374, text figs. 1-14, pls. 36-41, tables 1-21.

COLE LaMONT C., 1943.—Experiments on toleration of high temperature in lizards with reference to adaptive coloration. Ecology, Vol. 24, pp. 94-108, figs. 1-2, tables 1-4.

COWLES, RAYMOND B., and CHARLES M. BOGERT, 1944.—A preliminary study of the thermal requirements of desert reptiles. Bull. Amer. Mus. Nat. Hist., vol. 83, pp. 265-296, figs. 1-3, pls. 19-29.

HERTER, KONRAD, 1940.—Uber Vorzugstemperaturen von Reptilien. Zeitschr. Vergleich. Physiol., Vol. 28, nº 2, pp. 105-141.

KAUFFELD, CARL F., 1943.—Field notes on some Arizona reptiles and amphibians. Amer. Midland Nat., Vol. 29, pp. 342-359, figs. 1-2, pls. 1-2.

SHREVE, FORREST, 1942.—The desert vegetation of North America. Bot. Rev., Vol. 8, pp. 195-247, map.

SMITH, HOBART M., 1939.—The Mexican and Central American lizards of the genus **Sceloporus.** Zool. Ser. Field Mus. Nat. Hist., Vol. 26, pp. 1-397, 59 figs., 31 pls.

————, 1946.—Handbook of lizards. Lizards of the United States and Canada. Ithaca, New York, Comstock Publishing Co. xx+557 pp., 136 figs. 135, pls. 41 maps.

STEBBINS, ROBERT C., 1944.—Field notes on a lizard, the mountain swift, with special reference to territorial behavior. Ecology, Vol. 25, pp. 233-245, figs. 1-2.

THORNTHWAITE, C. W., 1931.—The climates of North America according to a new classification. Geogr. Rev., Vol. 21, pp. 633-655, figs. 1-13, map.

WOODBURY, MARIAN, and ANGUS M. WOODBURY, 1945.—Life-history studies of the sagebrush lizard **Sceloporus g. graciosus** with special reference to cycles in reproduction. Herpetologica, Vol. 2, pp. 175-196, figs. 1-3.