

Fall Reproductive Activity in the High Altitude Mexican Lizard, *Sceloporus Grammicus Microlepidotus*

Louis J. Guillette, Jr.¹ and Gustavo Casas-Andreu²

¹Laboratory of Comparative Reproduction, Department of Environmental, Population, and Organismic Biology,
University of Colorado, Boulder, Colorado 80309

²Laboratorio de Herpetología, Departamento de Zoología, Instituto de Biología, UNAM, A.P. 70-150,
México 20, D.F., México

ABSTRACT—*Sceloporus grammicus microlepidotus* is a viviparous, high altitude Mexican lizard. Specimens were obtained from several locations in the Parque Nacional de Zoquiapan, México, México. This species exhibits a reproductive cycle in which ovulation and fertilization occur during the fall and parturition the following spring. Vitellogenesis begins in late July in female *S. g. microlepidotus*, whereas the onset of testicular development occurs in February. Thus, it appears that male reproductive activity is initiated in spring, whereas female reproductive activity is initiated in the fall. The adaptive significance of fall courtship and mating in lizards is discussed.

* * *

INTRODUCTION

Studies in environmental reproductive physiology have established that temperate reptiles have a relatively short period of sexual activity, followed by a longer period of sexual inactivity and gonadal quiescence (reviewed by Fitch, 1970; Jones, 1978; Licht, 1972; Lofts, 1969; Mayhew, 1968; St. Girons, 1963). In many temperate lizards, the period of gonadal activity occurs during the spring and early summer months (Licht, 1972). An increasing number of reports, however, indicate that some temperate viviparous lizards are fall breeders; i.e., gametogenesis, courtship, mating and fertilization occur during the fall months. Embryonic development occurs during the winter, with parturition in the spring (*Gerrhonotus liocephalus infernalis*: Flury, 1949; *Liolaemus multiformis*: Pearson, 1954; Donoso-Barros, 1966; *Eumeces egregius*: Mount, 1963; *Sceloporus cyanogenys*: Crisp, 1964; *Sceloporus jarrovi*: Goldberg, 1970, 1971; *Sceloporus poinsetti*: Ballinger, 1973).

Complete or partial fall gonadal recrudescence without consequent courtship and mating has also been observed in temperate lizards. Species exist in which complete vitellogenesis occurs in the fall before brumation (*Scincella himalayana*: Duda and Koul, 1977) and those in which partial vitellogenesis occurs before brumation, with completion of ovarian development in the spring before courtship and mating (*Sceloporus graciosus*: Woodbury and Woodbury, 1945; *Leiopisma zelandia*: Barwick, 1959; *Hoplodactylus pacificus*: Fawcett, 1972; *Gerrhonotus kingi*: Goldberg, 1975; *Agama tuberculata*: Koul and Duda, 1977).

Smyth and Smith (1968) observed a unique reproductive cycle in *Hemiergis peronii*. In this species, the male exhibits complete testicular development in the fall, terminating in fall courtship and mating with females possessing quiescent ovaries. The sperm are stored by the female, and fertilization occurs in the spring following ovulation. Initiation of partial testicular development during the fall and winter is well known for a number of species and appears to be fairly common in temperate males (*Anolis carolinensis*: Fox and Dessauer, 1958; *Uma notata*, *Uma inornata*, *Uma scoparia*: Mayhew and Wright, 1970; *Holbrookia maculata maculata*: Cuellar and Fawcett, 1972; *Hoplodactylus pacificus*: Fawcett, 1972; *Sceloporus scalaris*: Newlin, 1976; *Uta stansburiana*: Goldberg, 1977).

Many lizards exhibiting fall breeding or fall gonadal growth occur at high altitudes. Considering the limited reports of fall breeding or fall gonadal activity in lizards, as well as the limited information concerning the reproductive biology of Mexican high altitude lizards, we felt it is of interest to report another species (*Sceloporus grammicus microlepidotus*) in which fall gonadal recrudescence and fertilization occurs.

Sceloporus g. microlepidotus is a viviparous sceloporine of moderate size (maximum SVL = 81 mm) inhabiting the pine forests of southern Mexico (Smith, 1939). This subspecies inhabits dead trees, stumps and logs in this area, and has been observed living as high as 4,120 m on Pico de Orizaba, Veracruz (Swan, 1952). The reproductive cycle of this lizard is unknown, although some relevant observations have been reported. Werler (1951) observed newborn young in the months of January to March at an altitude of 2300 m in Veracruz. Nongravid females were obtained in July by Davis and Dixon (1961), whereas Davis and Smith (1953) caught females from Tres Marias, Morelos, in August with large yolking oocytes (4 mm or less).

MATERIALS AND METHODS

Ten to twenty *S. g. microlepidotus* of both sexes were collected during the last week of each month (August 1978–July 1979) from several sites near the Campo Experimental de Zoquiapan, southeast of the Parque Nacional de Zoquiapan, México, México (19°41'30" N by 98°42'30" W). Specimens were collected between the altitudes of 2000–3200 m. Additional *Sceloporus g. microlepidotus* females were captured in May and held in the laboratory so that parturition could be observed.

The specimens were killed using chloroform and preserved in 10% neutral-buffered formalin. Information obtained on each animal consisted of (1) SVL (mm), (2) total body weight (g), (3) gonadal weight (g), (4) number of eggs or embryos per female, and (5) the developmental stage of each embryo. A gonadal-somatic index (GSI) was calculated by dividing the gonadal weight by the total body weight and multiplying by 100. These indices were then tabulated to obtain a mean and standard error for each month. A one-way ANOVA and Duncan's multiple range test were then performed to determine significant changes in the GSIs (Bruning and Kintz, 1977). A Pearson's product-moment correlation coefficient test was performed to determine the correlation between brood size and SVL of females (Bruning and Kintz, 1977). Embryos were categorized using the system developed by Lemus (1967) for the viviparous high altitude lizard *Liolaemus gravenholti*. Stages of development described herein are for embryos obtained at the end of each month. Specimens used in this study are deposited in the herpetology collections at the Universidad Nacional Autónoma de México, Mexico City, and the University of Colorado Museum, Boulder.

RESULTS

The reproductive cycle of *S. g. microlepidotus* is presented in Figure 1. Female *S. g. microlepidotus* exhibit fall gonadal development. Vitellogenesis begins in July and continues into early September when ovulation, fertilization, and blastodisc formation occur. Corpora lutea form after ovulation and remain visible until January, at which time they undergo a rapid size reduction. This reduction is reflected in the GSI which decreases significantly from 1.78 ± 0.39 to 0.67 ± 0.12 ($F(11,48) = 31.25$, $p < 0.05$). The ovarian GSI remains at this level until the onset of vitellogenesis the following July. Females give birth in May or June, after a gestation period of approximately 8 months. Brood sizes average 5.2 ± 0.25 young (range 3–7). A significant Pearson's correlation coefficient test indicated that brood size is dependent on female SVL; i.e., larger females have a larger number of young (Fig. 2). This relationship has been observed in other sceloporine lizards (Goldberg, 1971; Ballinger, 1978). The average SVL for females was 48.53 ± 0.76 (range 42.3–61.2).

The *S. g. microlepidotus* embryos show a reduced rate of development (embryonic diapause) during the late fall months. This phenomenon is well documented in *S. jarrovi*, a viviparous lizard exhibiting fall reproductive activity (Goldberg, 1970, 1971). The first observable embryonic development occurs in September with the formation of a blastodisc (Stage 2). No further detectable development occurs until November, when the blastodisc is segmented into an *area pellucida* and an *area opaca* (Stage 6). Development is rapid during December, with the formation of the cardiac region and the optic cup (Stage 19). The contracting heart, lens placode and auditory pit are visible during January (Stage 22). A mesenchyme bulge develops in February, which clearly defines the eyeball margin (Stage 25). By March, the limb buds and external nares are present (Stage 32). Scale formation and pigmentation appear during April (Stage 35), with parturition in May or June. Young are born surrounded by the amniotic sac, from which they emerge by lateral movements within 30 seconds.

It is interesting that the onset of testicular growth in *S. g. microlepidotus* occurs in spring (see Fig. 1). Maximum testicular GSI is reached in March or April. The testes remain enlarged until July. A significant ($F(11,48) = 35.65, p < 0.05$) decrease in testicular size is observed in August and September, with the testes remaining small until the following February. Territorial behavior by males was observed in early April and May, and was directed toward both sexes. We have not observed courtship or mating in the field. However, G. L. Góngora (personal communication) has observed both behaviors in *S. g. microlepidotus* during September. Males had an average SVL of 49.46 ± 1.02 (range 43.4–55.9).

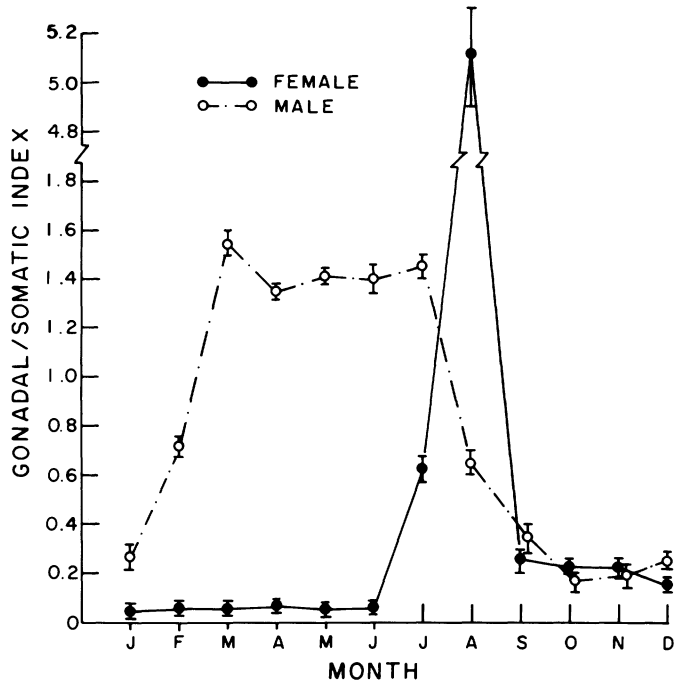


FIGURE 1. Monthly changes in the gonadal somatic index (gonad weight/body weight $\times 100$) for both sexes of *Sceloporus grammicus microlepidotus*, August 1978–July 1979. Values are $\bar{X} \pm SE$; $N = 5$.

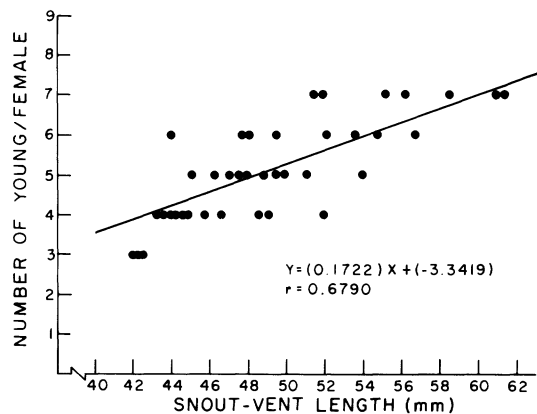


FIGURE 2. Correlation of the total number of embryos/eggs per female with body size (snout-vent length) in the lizard *Sceloporus grammicus microlepidotus*.

DISCUSSION

Sceloporus g. microlepidotus is reproductively active in the fall. Since courtship and mating are believed to occur in September, the epididymides could store sperm that inseminate the females in the fall. Sperm storage would be necessary as the testes are regressing at this time. The other

possibility, however, is that the courtship and mating periods could also occur earlier in the summer, with the female storing sperm until fall when ovulation occurs. Sperm storage by females, with subsequent fertilization of the ova by this sperm, has been reported in other reptilian species (see Fox, 1977). The solution to this question must await a histological study of the reproductive organs of this species and further field observations.

The reproductive cycle of *S. g. microlepidotus* differs markedly from a "normal" temperate lizard reproductive cycle, in which reproductive competence is reached by both sexes in the spring, as occurs in the viviparous lizard *Xantusia vigilis* (Miller, 1949) and many others (Fitch, 1970; Mayhew, 1968). This cycle also differs from a fall breeding pattern in which both testicular and ovarian development occur in late summer and early fall as in *S. jarrovi* (Goldberg, 1970). It is interesting to note that the male reproductive activity of *S. g. microlepidotus* is initiated in spring, whereas female reproductive development is initiated in the fall. This may suggest that the female and male reproductive systems are responding to different environmental stimuli.

It should also be noted that all three viviparous North American sceloporine lizards are fall breeders; i.e., gametogenesis, courtship, mating and fertilization occurs during the fall months (*Sceloporus cyanogenys*: Crisp, 1964; *S. jarrovi*: Goldberg, 1970, 1971; *S. poinsetti*: Ballinger, 1973). The significance of this relationship has not been investigated. Very few studies have been done concerning the relationship between fall breeding and environmental factors. This may be due to the fact that fall breeding has been viewed as a rare reproductive mode. It would appear, however, from evidence presented here and in previous studies, that fall breeding is not an uncommon reproductive mode used by viviparous temperate or high altitude lizards. Temperate oviparous lizards similarly may exhibit complete or partial fall gonadal recrudescence.

It has been suggested that fall reproductive activity is a strategy for producing young at the onset of the spring growing season, when food is plentiful (Goldberg, 1971). Young are born at the onset of a relatively short growing season, which will allow maximum growth and energy assimilation. Fall breeding would appear to be beneficial to the adults as well. By breeding in fall, adults utilize the complete spring and summer for energy storage and growth. Thus, this cycle may be advantageous for those lizards living at high altitudes or temperate regions where the growing season is short, ambient temperatures low, and *in utero* embryonic development relatively long.

A possible disadvantage to fall fertilization is that the female is gravid for an extended period of time. Thus energy is required by the female for an extended period: that is, if there is no embryonic diapause and development continues throughout the winter. Tinkle and Hadley (1975) have shown that the reproductive effort of *S. jarrovi*, a fall breeder, is higher per clutch than that of spring breeding oviparous lizards (reproductive effort is defined calorically as the ratio of calories invested in eggs in a given breeding season compared to the total calories expended by the individual's metabolism). A second possible disadvantage may be the depletion of the fat body stores. Goldberg (1972) has observed that the fat body stores of *S. jarrovi* are used for vitellogenesis in the fall. This utilization, however, was not complete, and the remaining stores were utilized during the winter months. Thus, partial use of the fat bodies for fall vitellogenesis may not be a disadvantage. Subsequent studies will be required to determine the prevalence of fall breeding and fall gonadal activity in other high elevation, viviparous reptiles.

ACKNOWLEDGMENTS

We would like to thank E. A. Guillette, R. E. Jones, H. M. Smith, D. Duvall, B. Pierce, D. O. Norris and A. Cruz for helpful critique of this manuscript, as well as A. Ramirez B. for assistance in obtaining lizards, and G. Flater for technical assistance. This research was supported in part by a grant from the Walker Van Riper Fund, University of Colorado Museum, to L. J. Guillette.

LITERATURE CITED

- Balinger, R. E. 1973. Comparative demography of two viviparous iguanid lizards (*Sceloporus jarrovi* and *Sceloporus poinsetti*). *Ecology* 54:269-283.

- . 1978. Variation in and evolution of clutch and litter size. *In*: R. E. Jones, ed. *The Vertebrate Ovary: Comparative Biology and Evolution*, Plenum Press, New York, pp. 789–819.
- Barwick, R. 1959. The life history of the common New Zealand skink *Leiopisma zelandia* (Gray, 1843). *Trans. Royal Soc. New Zealand* 86:331–380.
- Bruning, J. L. and B. Kintz. 1977. *Computational Handbook of Statistics*, 2nd ed., Scott Foresman and Company, Glenview, Illinois. 308 pp.
- Crisp, T. 1964. Studies of reproduction in the female ovoviparous iguanid lizard *Sceloporus cyanogenys* (Cope). *Texas J. Sci.* 16:481.
- Cuellar, H. and J. Fawcett. 1972. The male sexual cycle of the lesser earless lizard, *Holbrookia maculata maculata* (Reptilia: Iguanidae). *J. Colorado-Wyoming Acad. Sci.* 7: abstract 110.
- Davis, W. and J. Dixon. 1961. Reptiles (exclusive of snakes) of the Chiapancingo region, Mexico. *Proc. Biol. Soc. Washington*, 74:37–56.
- and H. M. Smith. 1953. Lizards and turtles of the Mexican state of Morelos. *Herpetologica* 9:100–108.
- Donoso-Barros, R. 1966. *Reptiles de Chile*. Edición de la Universidad de Chile. Santiago, 458 pp.
- Duda, P. L. and O. Koul. 1977. Ovarian cycle in high altitude lizards from Kashmir. Part II. *Scincella himalayana* (Boulenger). *Herpetologica* 33:417–433.
- Duellman, W. 1961. The amphibians and reptiles of Michoacan, Mexico. *Univ. Kansas Publ. Mus. Nat. Hist.* 15:1–148.
- Fawcett, J. 1972. The reproductive cycle of *Hoplodactylus pacificus* (Reptilia: Gekkonidae). *J. Colorado-Wyoming Acad. Sci.* 7: abstract 114.
- Fitch, H. 1970. Reproductive cycles in lizards and snakes. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* 52:1–247.
- Flury, A. 1949. *Gerrhonotus liocephalus infernalis* Baird in Texas. *Herpetologica* 5:65–67.
- Fox, H. 1977. The urogenital system of reptiles. *In*: Gans, C. and T. Parsons, eds. *Biology of the Reptilia*, Vol. 6, Academic Press, New York, pp. 1–158.
- Fox, W. and H. C. Dessauer. 1958. Response of the male reproductive system of lizards (*Anolis carolinensis*) to unnatural day lengths in different seasons. *Biol. Bull.* 115:421–439.
- Goldberg, S. 1970. Seasonal ovarian histology of the ovoviparous iguanid lizard *Sceloporus jarrovi* Cope. *J. Morphol.* 132:265–276.
- . 1971. Reproductive cycle of the ovoviparous iguanid lizard *Sceloporus jarrovi* Cope. *Herpetologica* 27:123–131.
- . 1972. Seasonal weight and cytological changes in the fat bodies and liver of the iguanid lizard *Sceloporus jarrovi* Cope. *Copeia* 1972:227–232.
- . 1975. Reproduction in the Arizona alligator lizard *Gerrhonotus kingii*. *S. W. Natur.* 20:412–413.
- . 1977. Reproduction in a mountain population of the side-blotched lizard, *Uta stansburiana* (Reptilia, Lacertilia, Iguanidae). *J. Herpetol.* 11:31–35.
- Jones, R. E. 1978. Ovarian cycles in nonmammalian vertebrates. *In*: *The Vertebrate Ovary: Comparative Biology and Evolution*, ed. R. E. Jones. Plenum Press, New York, pp. 731–762.
- Koul, O. and P. L. Duda. 1977. Ovarian cycle in high altitude lizards from Kashmir. *Copeia* 1977:751–754.
- Lemus, D. A. 1967. Contribution al estudio de la embriología de reptiles chilenos. II. Table de desarrollo de la lagartija vivípara *Liolaemus gravenhorti* (Reptilia; Squamata; Iguanidae). *Biologica* 40:39–61.
- Licht, P. 1972. Environmental physiology of reptilian breeding cycles: Role of temperature. *Gen. Comp. Endocrin. Suppl.* 3:447–488.
- Lofts, B. 1969. Seasonal cycles in reptilian testes. *Gen. Comp. Endocrin. Suppl.* 2:147–155.
- Mayhew, W. 1968. *Biology of desert amphibians and reptiles*. *In*: G. W. Brown, Jr., ed., *Desert Biology*, Vol. I., Academic Press, New York, pp. 195–356.
- and S. J. Wright. 1970. Seasonal changes in testicular histology of three species of lizard genus *Uma*. *J. Morph.* 130: 163–186.
- Miller, M. 1948. The seasonal histological changes occurring in the ovary, corpus luteum and testis of the viviparous lizard, *Xantusia vigilis*. *Univ. California Publ. Zool.* 47:197–224.
- Newlin, M. 1976. Reproduction in the bunch grass lizard, *Sceloporus scalaris*. *Herpetologica* 32:171–184.
- Pearson, O. 1954. Habits of the lizard *Liolaemus multiformis multiformis* at high altitudes in southern Peru. *Copeia* 1954:111–116.
- Smith, H. M. 1939. The Mexican and Central American lizards of the genus *Sceloporus*. *Zool. Ser., Field Mus. Nat. Hist.* 26:1–397.
- Smyth, M. and M. Smith. 1968. Obligatory sperm storage in the skink *Hemiergis peronii*. *Science* 161:575–576.
- Stebbins, R. C. 1958. A new alligator lizard from the Paramint Mountains, Inyo County, California. *Amer. Mus. Novit.* #1883, 27 pp.
- St. Girons, H. 1963. Spermatogénèse et évolution cycliques des caractères sexuels secondaires chez les Squamata. *Ann. Sci. Nat.* 12:461–478.
- Swan, L. 1952. Some environmental conditions influencing life at high altitude. *Ecology* 33:109–111.
- Tinkle, D. and N. Hadley. 1975. Lizard reproductive effort: Caloric estimates and comments on its evolution. *Ecology* 56:427–434.
- Werler, J. E. 1951. Miscellaneous notes on the eggs and young of Texan and Mexican reptiles. *Zoologica* 36:37–48.
- Woodbury, M. and A. M. Woodbury. 1945. Life history of the sagebrush lizard *Sceloporus g. graciosus* with special reference to cycles in reproduction. *Herpetologica* 2:175–196.

Accepted 6 Nov 1979

Copyright 1980 Society for the Study of Amphibians and Reptiles

