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THE REPRODUCTIVE BIOLOGY OF THE HIGH ELEVATION MEXICAN LIZARD *BARISIA IMBRICATA*

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ABSTRACT: *Barisia imbricata* is a high elevation viviparous lizard occurring in the transvolcanic mountains of Mexico. The reproductive biology of one subspecies (*B. imbricata imbricata*) is described in detail whereas partial information is presented for the other three subspecies. Male *B. i. imbricata* exhibit testicular recrudescence in spring, peak activity during the summer, and regression in autumn. Testicular recrudescence is positively correlated with increasing photoperiod and precipitation of the collection area but is not correlated with temperature. Females exhibit a summer/autumn activity pattern with follicular growth in summer, ovulation in autumn, and pregnancy over the winter months. Follicular growth is positively correlated with the onset of summer precipitation but is not correlated with rising temperature or increasing photoperiod. Dry mass of ovulated eggs and neonates suggests that the placenta of this species has a nutritive function. Data on the other subspecies indicate that little geographic variation exists in the reproductive cycle.

Key words: Reptilia; Sauria; Anguidae; *Barisia imbricata*; Reproduction; Viviparity; Placentation

THE reproductive cycle of a species is an important indicator of the reproductive strategy of a species. Within reptiles, this is especially evident, as reproductive activity is correlated with any number of environmental cues (Duvall et al., 1982). In many species, reproductive activity exhibits a cyclical pattern. That is, periods of reproductive activity occur, followed by relatively longer quiescent periods. Until quite recently, a paradigm existed indicating that temperate squamates exhibited reproductive activity during the spring and summer months (Fitch, 1970). However, studies are now available which suggest that diverse patterns of reproductive activity exist in temperate zone lizards of North America (for review see Guillette and Casas-Andreu, 1980). A distinction between the reproductive patterns of oviparous and viviparous species is developing. That is, some temperate viviparous lizards exhibit a typical spring and summer reproductive activity pattern (*Gerrhonotus coeruleus*: Stewart, 1979; Vitt, 1973; *Xantusia vigilis*: Miller, 1951) although some gonadal activity may occur during the autumn months (*X. vigilis*: Miller, 1951). In contrast, other temperate, viviparous species exhibit an autumn reproductive activity pattern (*Sceloporus cyanogenys*: Callard et al., 1972; Crisp, 1964; *Sceloporus jarrovi*: Ballinger, 1973; Goldberg, 1970; *Sceloporus poinsetti*: Ballinger, 1973; *Sceloporus grammicus*: Guillette and Bearce, 1986; Guillette and Casas-Andreu, 1980; Ortega and Barbault, 1984; *Sceloporus formosus*: Guillette and Sullivan, 1985; *Sceloporus mucronatus*: Mendez de la Cruz and Villagran Santa Cruz, 1983; *Eumeces copei*: Guillette, 1983). Moreover, in several of the aforementioned species, asynchrony may exist between male and female reproductive activity, with males exhibiting gonadal activity (spermatogenesis and spermiogenesis) in spring whereas ovarian activity (vitellogenesis, ovulation) occurs in autumn. Recently, Vial and Stewart (1985) described a unique reproductive cycle in the tropical viviparous lizard, *Barisia monticola*. They observed that the males exhibited continuous spermatogenic activity, whereas the ovarian cycle is biennial. The females ovulate in autumn and are pregnant for an extended period of time (4–5 mo). Thus, a diversity of patterns exists.

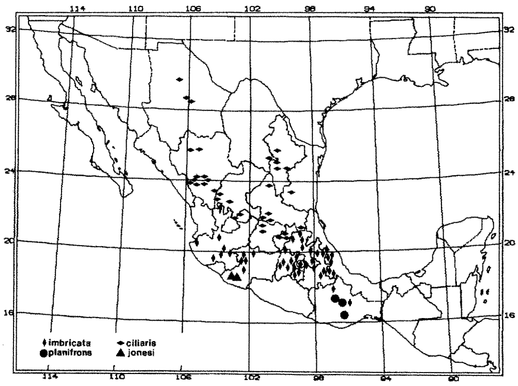

FIG. 1.—Distribution of the four subspecies of the Mexican lizard *Barisia imbricata*.

The environmental control of these patterns requires study. Several environmental factors appear important as controllers of reptilian reproductive activity, including temperature, photoperiod and precipitation (for review see Duvall et al., 1982). Among male squamates, testicular recrudescence is stimulated by increasing or decreasing ambient temperature (see Licht, 1972, 1984; Marion, 1982, for review). The control of ovarian activity, however, appears more complex, with temperature, photoperiod and food availability all exerting important influences (see Duvall et al., 1982, for review).

Examination of geographically wide-ranging species may provide important information on variability and control of the reproductive cycle. *Barisia imbricata* is such a species, occurring throughout the central highlands of Mexico (Guillette and Smith, 1982). Previous studies examining wide-spread species have noted a strong phylogenetic component; that is, although populations are geographically wide-spread, a strong conservatism exists in basic reproductive strategy (Ballinger, 1983). Additional studies are needed to examine the degree of reproductive flexibility species exhibit in differing environmental conditions.

Four subspecies of *Barisia imbricata* are recognized (*B. i. imbricata*, *B. i. ciliaris*, *B. i. planifrons*, *B. i. jonesi*); all are viviparous and occur at high elevations (Guillette and Smith, 1982). Specific ranges for each subspecies are given in Guillette and Smith (1982, appendix) but in general they are as follows (Fig. 1): *B. i. imbricata*—the transvolcanic mountains in the central Mexican states of Distrito Federal, Hidalgo, Jalisco, México, Michoacán, Morelos, Oaxaca, Puebla and Veracruz; *B. i. ciliaris*—ranges throughout the central plateau in the states of Chihuahua, Coahuila, Durango, Guanajuato, Hidalgo, Nuevo León, Queretaro, San Luis Potosí, Tamaulipas and Zacatecas; *B. i. planifrons*—restricted in range to the mountains of central and southern Oaxaca; *B. i. jonesi*—inhabits the pine forests of the Sierra de Coalcomán, Michoacán only. Few data are available concerning reproductive activity for this species. Stebbins (1958) obtained a female with very advanced embryos ready for birth on 4 May. These data indicate autumn reproductive activity or very early spring activity and rapid embryonic development. *Barisia imbricata* is a terrestrial, thermophilic lizard with a low mean body temperature (Guillette, unpublished data), suggesting that rapid embryonic growth is unlikely.

This study was designed to examine the following questions. (1) How much variation exists in the reproductive cycles of the four subspecies? (2) Does this viviparous species exhibit autumn reproductive activity as do other high elevation Mexican viviparous lizards? (3) Do the females contribute any nutrients to the young during in utero development?

MATERIALS AND METHODS

Male and female *Barisia imbricata imbricata* were collected monthly from several sites in the Mexican states of México, Morelos and Distrito Federal at altitudes of 3000–3400 m. Animals were killed and preserved in 10% neutral buffered formalin. Initial data obtained on each animal consisted of (1) snout–vent length (SVL), (2) total body mass (g), and (3) date of capture. Following death, the abdomen was incised and gonads were exposed. In females, the largest ovarian follicle was measured, vitellogenic follicles were counted if present, and the presence and number of corpora lutea were recorded.

The number of eggs or embryos per female was noted as well as the developmental stage (Defaure and Hubert, 1961) of the embryos. Newly ovulated eggs and eggs containing variously staged embryos were collected and weighed. They then were dried in an oven at 60 C until three constant masses were obtained. The right ovary of each animal was removed, dehydrated, embedded in paraffin, and sectioned at 10 μm. Sections were stained with Alcian Blue and were counterstained with Hematoxylin and Eosin. Slides were examined to determine stage of vitellogenesis, follicular atresia, and luteal stage. Within males, the longest and shortest testicular axes were measured and a testicular volume (V) was calculated using the formula for the volume of an ellipsoid:

$$V = \frac{4}{3} \pi a^2 b$$

where a is ½ the shortest diameter and b is ½ the longest diameter. These indices were tabulated to obtain a monthly mean and standard error. A one-way ANOVA and Duncan's multiple range test were performed to determine significant differences in monthly values. A Pearson's product-moment correlation coefficient test was performed to determine if any correlation existed between litter size and SVL of females, and gonadal activity with environmental conditions in either sex. We used $\alpha = 0.05$ for statistical significance. Precipitation and temperature data were obtained from García (1981), and photoperiod data were obtained from the Astronomical Almanac (1984).

In addition to the specimens collected in the field, museum specimens also were examined. Specimens of all the subspecies were obtained and analyzed using the methods described above (exclusive of the histological examinations). A list of the museum specimens used and the location of their capture was presented in Guillette and Smith (1982, appendix).

RESULTS

Barisia i. imbricata

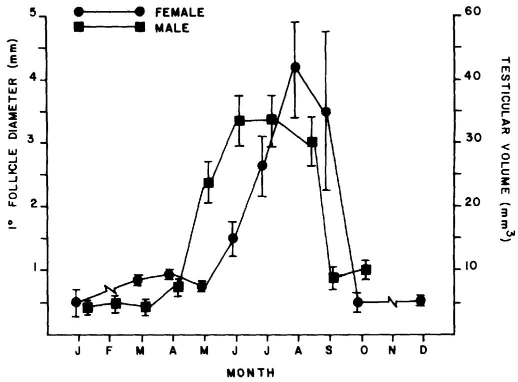

FIG. 2.—Monthly changes in primary follicular diameter and testicular volume of the viviparous lizard, *Barisia i. imbricata*. Values represent the mean ± 1 SE.

Reproductive cycles of male and female *B. i. imbricata* are displayed in Fig. 2. These data represent information from both field ($n = 40$) and museum ($n = 118$) animals. No significant differences were noted between field and museum animals for any parameter measured. An increase in variance was observed in the museum specimens, but this represented less than 1 SE of the mean. Thus, the two data sets were treated as one.

Females exhibit a summer/autumn activity pattern, with follicular growth beginning in June and ovulation occurring during late August and September (Fig. 2). Ovarian activity is correlated with precipitation ($r = 0.829$, $P < 0.01$) for the Río Frío, México, México area (Fig. 3), but not with either mean monthly temperature ($r = 0.21$, $P > 0.05$) or photoperiod ($r = 0.09$, $P > 0.05$). Females are pregnant throughout the winter and early spring (October–April). Average clutch size is 6.9 ± 0.35 (±1 SE; $n = 35$ clutches) based on in utero eggs. However, a count of vitellogenic follicles indicates a projected mean clutch size of 10.0 ± 1.1 ($n = 20$). These data indicate an atresia rate of 29% for vitellogenic follicles. A significant correlation does not exist between clutch size and female SVL ($r = 0.326$, $P > 0.05$). However, an inverse correlation exists between clutch size and neonate wet mass ($r = 0.714$, $P < 0.05$, $n = 35$). Egg volume at ovulation is 230.9 ± 29.7 mm^3 with a wet mass of 424.9 ± 16.6 mg and a dry mass of 219.9 ± 9.5 mg. The ratio between

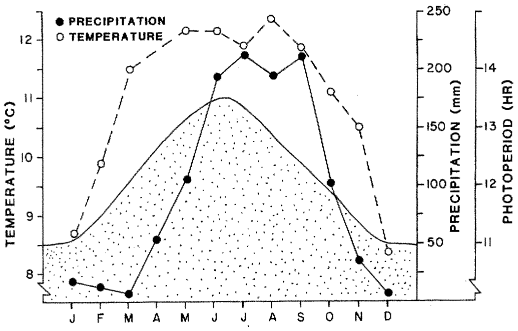

FIG. 3.—Monthly mean temperature and precipitation values and photoperiod for the study area (Río Frío, México, México). The shaded area represents the length of the photophase.

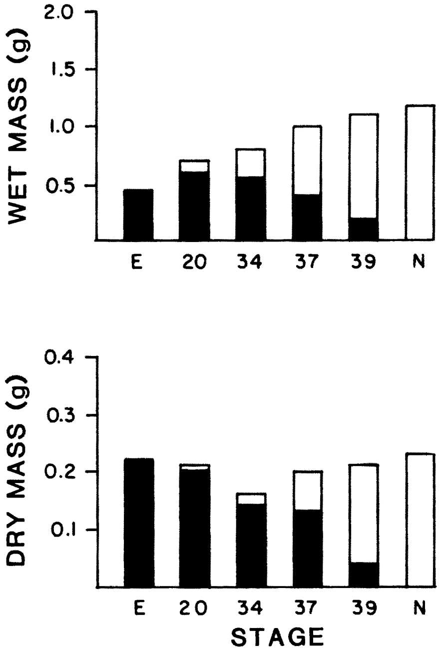

FIG. 4.—Mean egg and embryo wet and dry masses throughout the pregnancy cycle (selective stages). Egg mass = shaded area; embryonic mass = clear area.

egg/embryo mass changes throughout gestation (Fig. 4). At birth, neonates have a mean SVL of 29.1 ± 0.5 mm, with a mean wet mass of 783.0 ± 71.8 mg and dry mass of 223.0 ± 40.2 mg (Fig. 4). Embryonic growth exhibits a two-phase pattern. During early embryonic development, very little increase in mass occurs. In fact, embryonic mass does not increase appreciably until late in development (Fig. 4) when embryos exhibit a rapid increase in growth rate. During winter, embryonic growth is relatively slow with development reaching stage 20 by late February. However, during March and April, development and growth are rapid with parturition occurring in May. The smallest reproductively active female had a SVL of 77.5 mm; reproductively active females ranged in size from 77.5–124.7 mm and were not significantly different in size from males (Fig. 5).

Histological examination of the ovaries revealed that vitellogenesis begins in follicles 2.0 mm in diameter. Atresia is common in histological preparations of vitellogenic follicles and occurs at a rate (27.5%) similar to that suggested by the clutch size data reported above. Corpora lutea form from each ovulated follicle and remain active until embryonic stage 30. They then begin to regress in size and luteolysis is complete by parturition.

Males exhibit a pattern of testicular recrudescence in spring (April–May), peak activity in summer (June–August) and a rapid regression in September (Fig. 2). The period of courtship and mating is unknown. Very little variation in reproductive cyclicity exists among males. Testicular recrudescence is correlated with the photoperiod for 19 N latitude ($r = 0.9511$, $P < 0.01$) and with the precipitation cycle for Río Frío, México, México, the collection site ($r = 0.9921$, $P < 0.01$; Fig. 3). No significant correlation exists between any part of the male cycle and mean monthly temperature. The smallest male with enlarged testes was 87.1 mm SVL; reproductively active males ranged in size from 87.1–148.8 mm SVL. No sexual dimorphism in size was noted, because reproductively active males and females have the same mean lengths (female = 102.3 ± 3.0; male = 102.3 ± 1.7; $n = 125$; Fig. 5). Moreover, the distributions of size classes were similar (Fig. 5).

Barisia i. ciliaris

Data obtained from museum specimens ($n = 18$ males and 38 females) concerning the reproductive cycle in *B. i. ciliaris* are

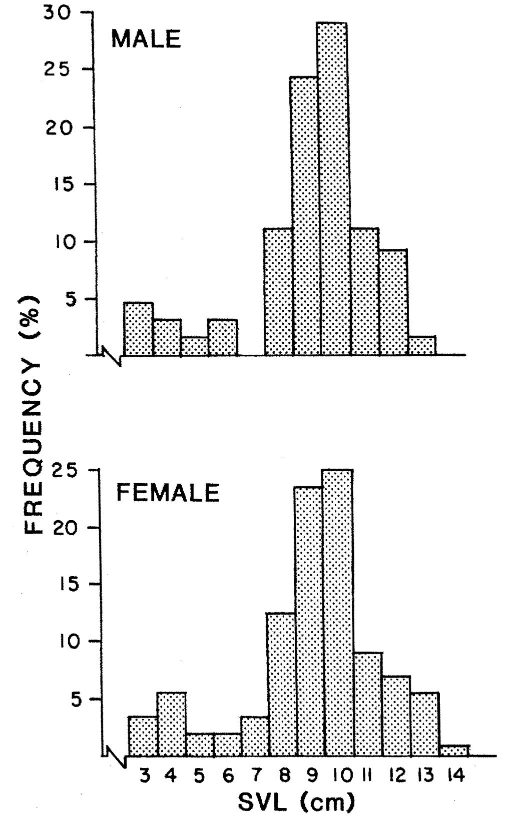

FIG. 5.—Size distribution for male and female *Barisia i. imbricata*.

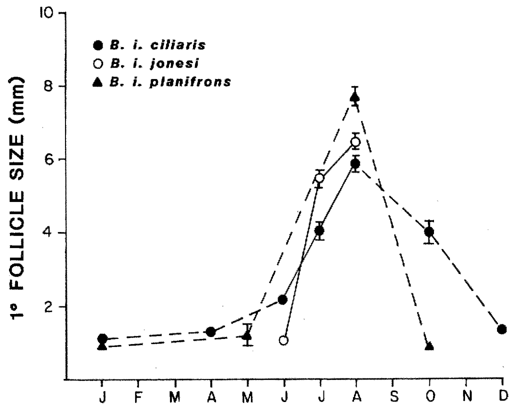

FIG. 6.—Partial reproductive cycle data for females from three subspecies of *Barisia imbricata*.

presented in Figs. 6 and 7. Females appear to exhibit a cycle similar to that described for *B. i. imbricata*. Follicular development and vitellogenesis occur between July and October, with most females exhibiting pregnancy by October (Fig. 6). Embryonic development occurs at a slow rate during the winter months (embryos are at stages 15–18 during December, 20–22 during January). Rapid development occurs between January and April. All females are post-partum in June. Mean clutch size determined from in utero eggs/embryos is 6.9 ± 0.5 ($n = 11$) whereas females have a mean of 11.4 ± 1.6 ($n = 6$) vitellogenic follicles. These data suggest a 39.5% atresia rate for vitellogenic follicles but should be viewed with caution due to the small sample size. A significant correlation between female SVL and clutch size is not exhibited ($r = 0.533$, $P > 0.05$) although a positive trend is evident. Reproductively active females ranged in size from 82.8–110.9 mm SVL.

Male activity is difficult to describe as data are available from a limited sample (3 mo data only). The data do suggest that male *B. i. ciliaris* exhibit a cycle similar to that of *B. i. imbricata* with summer testicular activity and autumn quiescence (Fig. 7). Reproductively active males range in SVL from 75.3–132.2 mm ($n = 14$).

Barisia i. jonesi

Reproductive cycle data were obtained on 26 museum specimens (12 males and 14 females) and are displayed in Figs. 6 and 7. Data are available for only 3 mo for females but suggest a pattern similar to that for the other subspecies already described. Ovarian activity is minimal in June with vitellogenesis occurring in July and August (Fig. 6). Only five pregnant females were examined, so no regression analysis was performed on clutch size and SVL. Mean clutch size as determined from in utero eggs and embryos was 7.2 ± 0.4 ($n = 5$). It was of interest that the female obtained in June was still pregnant, having seven pigmented young at stages 37–38, indicating imminent parturition. Fetal SVL's ranged from 29.8–31.2 mm ($n = 7$). Neonates obtained in June averaged 32.5 mm SVL whereas those from July are 38.8 mm in SVL. Reproductively active females exhibited SVL's of 90.3–105.3 mm.

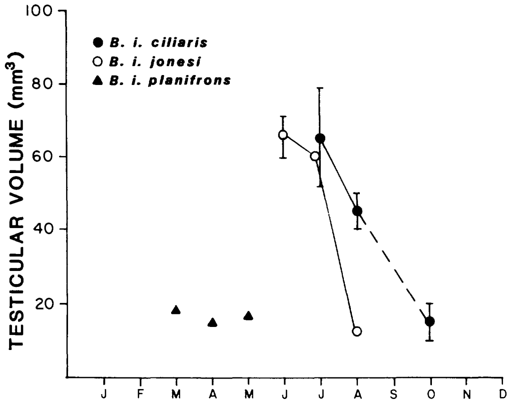

FIG. 7.—Partial reproductive cycle data for males of three subspecies of *Barisia imbricata*.

Males exhibit a reproductive activity cycle similar to that already described (Fig. 7). Maximal testicular volume appears to occur in summer (June–July) with rapid regression in August. The smallest reproductively active male examined was 88.5 mm SVL whereas the largest male was 131.2 mm SVL (n = 11).

Barisia i. planifrons

Only nine of the 21 (five males, 16 females) specimens examined were reproductively active. Females exhibit vitellogenesis in August and are pregnant in October, January and May (Fig. 6). Mean clutch size is 7.7 ± 1.4 (n = 6). Reproductively active females ranged from 101.3–108.0 mm SVL. No reproductively active males were obtained (Fig. 7).

DISCUSSION

Female *Barisia i. imbricata* exhibit a pattern of reproductive activity in which ovulation occurs during the autumn months and pregnancy occurs over the winter. This pattern is not unique among high elevation Mexican squamates (Guillette, 1983; Guillette and Casas-Andreu, 1980; Guillette and Sullivan, 1985; Mendez de la Cruz and Villagran Santa Cruz, 1983). In fact, this may be a common reproductive activity pattern for many viviparous, high elevation lizards. Species from three squamate families (Iguanidae, Scincidae, Anguidae) exhibit this pattern (see references above and this work). Tropical viviparous species (e.g., *Barisia monticola*) may not follow this pattern but may exhibit extensive periods of reproductive activity or lack cyclicity completely (e.g., the males of this species). However, females ovulate in the autumn and are pregnant during the "winter" months as are the temperate forms.

It is of interest that the reproductive cycle of both male and female *B. i. imbricata* is correlated with precipitation. Numerous studies have suggested that photoperiod and temperature are the most important environmental cues for timing reproductive activity in temperate lizards (for review see Duvall et al., 1982). Licht (1972) and Marion (1982) demonstrated that temperature was the cue stimulating testicular activity in *Anolis carolinensis* and *Sceloporus undulatus*, respectively. It is unlikely that rising temperature is the initial stimulatory signal in some autumn breeders (i.e., *Sceloporus jarrovi, S. poinsetti*) as testicular recrudescence occurs after peak ambient temperature. Warm ambient temperature may serve as a permissive agent allowing normal enzyme activity which is associated with spermatogenesis. The actual stimulus may be another factor, such as photoperiod or precipitation. Among temperate populations, photoperiod has been suggested as a major initiator of reproductive activity along with temperature. In contrast, precipitation has been viewed as important in tropical environments (for discussion see Fitch, 1970, 1982). The data presented for *B. i. imbricata* indicate that precipitation also may be important for temperate lizard populations as suggested by Ballinger (1977). Presumably, food availability increases with the onset of the rainy season. Thus, this period would be the optimal period for vitellogenesis. That is, adequate food appears very important for normal testicular and ovarian function (Cuellar, 1973; Greenberg and Gist, 1985; Hahn and Tinkle, 1965). Likewise, young born early in the growing season would have the maximum amount of time for feeding and growth before the onset of the next winter. The attainment of maximal size would increase the survivorship of the young (Ballinger, 1973).

Egg and neonate weight indicate that nutrient exchange occurs between mother and fetus. That is, the dry mass of the ovulated egg is similar to the dry mass of the neonate/late stage fetus. During normal embryonic development in reptiles, a loss of as little as 20%(Stewart and Castillo, 1984) or as great as 40% (Guillette, 1981*b*) of the dry mass between ovulated egg and neonate is not uncommon. No loss indicates that additional energy is being supplied to replace that which is used for somatic maintenance during development. Viviparous squamates have placentae capable of transporting ions, water and gases (Stewart and Castillo, 1984; Thompson, 1981, 1982; reviewed by Yaron, 1985). Several viviparous lizards, *Chalcides* (*Seps*) *chalcides*, *Leiolopisma* (*Lygosoma*) *weeksae*, *L.* (*L.*) *entrecasteauxi* (Weekes, 1935), *Xantusia vigilis* (Yaron, 1977) and snakes, *Thamnophis sirtalis* (Clark et al., 1955; Clark and Sisken, 1956; Hoffman, 1970) and *Suta* sp., *Austrelaps* sp. (= *Denisonia* sp.) (Weekes, 1935), exhibit placental nutrient exchange. Exchange of nutrients may be minimal or extensive, as in the lizard *Mabuya heathi* in which placental transport accounts for greater than 99% of the dry mass of the neonate (Blackburn et al., 1984). Placental exchange in *Barisia* appears moderate and future studies examining the placental unit of this species are needed.

No correlation between SVL and clutch size was observed in either *B. i. imbricata* or *B. i. ciliaris* females. This is uncommon in squamates, except for special cases (Anoline lizards and Sphaerodactyline geckos; Fitch, 1970). These data imply that female body size does not strongly influence the recruitment of follicles but that other factors are important. We noted that neonate size is inversely correlated with female body size. These data are similar to the findings of Stewart (1979) for the viviparous lizard *Gerrhonotus coeruleus*. Stewart (1979) presented a hypothesis suggesting that reproductive resources may be partitioned into either larger young or larger clutches. Thus, selection for one affects the other. That is, in *Barisia imbricata* and *Gerrhonotus coeruleus*, larger neonate size is selected for and clutch size decreases. Ballinger (1973) observed that larger young from viviparous female *Sceloporus jarrovi* exhibit greater survivorship. The above hypothesis centers on the premise of a relatively fixed energy budget. As mentioned above, several studies have demonstrated that nutrition is an important factor in ovarian activity, especially vitellogenesis (Greenberg and Gist, 1985; Hahn and Tinkle, 1965). It is also of interest that 25–30% of the follicles which begin vitellogenesis become atretic. However, no data correlating nutritional stage with atresia are available. *Barisia imbricata* has two germinal beds per ovary (Jones et al., 1982). Germinal beds are small regions on the dorsal ovarian surface containing dividing oogonia, naked oocytes, and primordial follicles. Atresia can occur at any stage of follicular growth in lizards but is most common in large, vitellogenic follicles (Byskov, 1978). We observed that atresia was most common in *Barisia* during vitellogenesis as well. Thus, atresia rather than fewer growing follicles accounts for the low instantaneous fecundity exhibited by this species. That is, atresia reduces the clutch size in *Barisia* by 25%. This reduction in clutch size may be in response to or a protoadaptation to viviparity. Previous studies have suggested that no difference in clutch size exists between oviparous and viviparous species (Guillette, 1981*a*; Tinkle et al., 1970). However, Guillette (1981*b*) noted that clutch size decreases with the evolution of viviparity in the lizard *Sceloporus bicanthalis*. Ovulated eggs double in size as demonstrated in this study (due primarily to the uptake of water; Thompson, 1981, 1982), and this factor may limit the number of young a female can retain. This is particularly relevant in the genus *Barisia* which possesses osteodermic scales and lateral folds which constrain body expansion.

Although data are sparse on two of the four subspecific populations, they suggest that all populations exhibit a similar pattern of reproductive activity. Previous studies examining the wide-ranging oviparous lizard species *Sceloporus undulatus* (Crenshaw, 1955; Ferguson et al., 1980; Tinkle, 1972; Tinkle and Ballinger, 1972; Vinegar, 1975) have provided large amounts of data on geographically-induced demographic variation in reproductive strategies. Modification of the reproductive biology is possible in viviparous populations as well, as in the Mexican lizard *Sceloporus grammicus* (Guillette and Bearce, 1986; Guillette and Casas-Andreu, 1980; Ortega and Barbault, 1984). In this species, males exhibit summer/autumn (Guillette and Bearce, 1986; Ortega and Barbault, 1984) or spring/summer (Guillette and Casas-Andreu, 1980) reproductive activity. That is, spring/summer activity is exhibited by the southernmost populations and summer/autumn activity by more northern populations. This pattern appears to reflect the precipitation patterns, and thus food availability, in these regions, because it is not correlated with temperature or photoperiod. In addition to cycle differences, other changes occur in clutch size, gonadal size, and the SVL-clutch size relationship among populations of *S. grammicus*. It is interesting that so little variation exists among the widely distributed populations of *B. imbricata*. Future studies examining other wide-ranging species are needed to determine if patterns in the variability of reproductive cycles occur within or among genera.

RESUMEN

Barisia imbricata es una lagartiga vivípara que habita a altas elevaciones en los montañas transvolcánicas de México. Se describe en detalle la biología reproductiva de una subespecie (*B. imbricata imbricata*), y se presenta informacíon parcial para las otras tres subespecies. Los machos de *B. i. imbricata* exhiben recrudescencia testicular en la primavera, actividad máxima durante el verano y regresión en el ontoño. La recrudescencia testicular se correlaciona positivamente con aumentos en el fotoperíodo y la precipitación en el área de colección, pero no se correlaciona con la temperatura. Las hembras exhiben un patrón de actividad verano/otoño, con crecimiento folicular en el verano, ovulación en el otoño y preñez durante los meses de invierno. El crecimiento folicular se correlaciona positivamente con el comienzo de las lluvias en el verano, pero no se correlaciona con el aumento en la temperatura o el fotoperíodo. La masa seca de los huevos ovulados y de los neonatos sugiere que la placenta tiene una función nutritiva en esta especie. Los datos para las otras subespecies indican que existe poca variación geográfica en el ciclo reproductivo.

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LITERATURE CITED

THE ASTRONOMICAL ALMANAC. 1984. U.S. Government Printing Office and Her Majesty's Stationery Office, Washington/London.

BALLINGER, R. 1973. Comparative demography of two viviparous lizards (*Sceloporus jarrovi* and *S. poinsetti*). Ecology 54:269–283.

———. 1977. Reproductive strategies: Food availability as a source of proximal variation in a lizard. Ecology 58:628–635.

———. 1983. Life history variations. Pp. 241–260. *In* R. B. Huey, E. R. Pianka, and T. W. Schoener (Eds.), Lizard Ecology: Studies of a Model Organism. Harvard University Press, Cambridge.

BLACKBURN, D. G., L. J. VITT, AND C. A. BAUCHOT. 1984. Eutherian-like reproductive specializations in a viviparous reptile. Proc. Nat. Acad. Sci., U.S.A. 81:4860–4863.

BYSKOV, A. G. 1978. Follicular atresia. Pp. 533–562. *In* R. E. Jones (Ed.), The Vertebrate Ovary: Comparative Biology and Evolution. Plenum Press, New York.

CALLARD, I. P., W. C. CHAN, AND M. ANDERSON POTTS. 1972. The control of the reptilian gonad. Am. Zool. 12:273–287.

CLARK, H., B. FLORIO, AND R. HUROWITZ. 1955. Embryonic growth of *Thamnophis sirtalis* in relation to fertilization date and placenta formation. Copeia 1955:9–13.

CLARK, H., AND B. F. SISKEN. 1956. Nitrogenous excretion by embryos of the viviparous snake *Thamnophis s. sirtalis*. J. Exp. Biol. 33:384–393.

Crenshaw, J. W. 1955. The life history of the southern spiny lizard, *Sceloporus undulatus undulatus* Latreille. Am. Midl. Nat. 55:257–298.

Crisp, T. M. 1964. Studies of reproduction in the female ovoviviparous lizard *Sceloporus cyanogenys* (Cope). Texas J. Sci. 16:481.

Cuellar, H. S. 1973. Effect of adiposectomy and feeding level on FSH-induced testicular growth in male lizards *Anolis carolinensis* (Reptilia: Iguanidae). J. Exptl. Zool. 185:65–72.

Dufaure, J. P., and J. Hubert. 1961. Table de développement du lézard vivipare: *Lacerta (Zootoca) vivipara* Jacquin. Arch. Anat. Microscop. Morphol. Exp. 50:309–328.

Duvall, D., L. J. Guillette, Jr., and R. E. Jones. 1982. Environmental control of reptilian reproductive cycles. Pp. 201–231. *In* C. Gans and F. H. Pough (Eds.), Biology of the Reptilia, Vol. 13D. Academic Press, New York.

Ferguson, G. W., C. H. Bohlen, and H. P. Woolley. 1980. *Sceloporus undulatus*: Comparative life history and regulation of a Kansas population. Ecology 61:313–322.

Fitch, H. S. 1970. Reproductive cycles in lizards and snakes. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 52:1–247.

———. 1982. Reproductive cycles in tropical reptiles. Occ. Papers Mus. Nat. Hist. Univ. Kansas 96: 1–53.

García, E. 1981. Modificaciones al sistema de clasificación climática de Köppen, 3rd Ed. Instituto de Geografía, U.N.A.M., México.

Goldberg, S. R. 1970. Seasonal ovarian histology of the ovoviviparous iguanid lizard *Sceloporus jarrovi* Cope. J. Morphol. 132:265–276.

———. 1971. Reproductive cycle of the ovoviviparous iguanid lizard *Sceloporus jarrovi* Cope. Herpetologica 27:123–131.

Greenberg, D. S., and D. H. Gist. 1985. Fat bodies and reproduction in female *Anolis carolinensis*. J. Exptl. Zool. 233:277–283.

Guillette, L. J., Jr. 1981*a*. Reproductive Strategies and the Evolution of Viviparity in Two Allopatric Populations of the Mexican Lizard, *Sceloporus aeneus*. Ph.D. Dissertation, University of Colorado, Boulder.

———. 1981*b*. On the occurrence of oviparous and viviparous forms of the Mexican lizard, *Sceloporus aeneus*. Herpetologica 37:11–15.

———. 1983. Notes concerning the reproduction of the montane skink, *Eumeces copei*. J. Herpetol. 17:144–148.

Guillette, L. J., Jr., and D. A. Bearce. 1986. Reproductive and fatbody cycles in the lizard, *Sceloporus grammicus disparalis*. Trans. Kansas Acad. Sci.: 89:31–39.

Guillette, L. J., Jr., and G. Casas-Andreu. 1980. Fall reproductive activity in the high altitude Mexican lizard, *Sceloporus grammicus microlepidotus*. J. Herpetol. 14:143–147.

Guillette, L. J., Jr., and H. M. Smith. 1982. A review of the Mexican lizard *Barisia imbricata*, with the description of a new subspecies. Trans. Kansas Acad. Sci. 85:13–33.

Guillette, L. J., Jr., and W. P. Sullivan. 1985. Reproductive and fatbody cycles of the lizard, *Sceloporus formosus*. J. Herpetol. 19:474–480.

Hahn, W. E., and D. W. Tinkle. 1965. Fat body cycling and experimental evidence for its adaptive significance to ovarian follicle development in the lizard *Uta stansburiana*. J. Exptl. Zool. 158:79–86.

Hoffman, L. H. 1970. Placentation in the garter snake *Thamnophis sirtalis*. J. Morphol. 131:57–88.

Jones, R. E., T. Swain, L. J. Guillette, Jr., and K. T. Fitzgerald. 1982. The comparative anatomy of lizard ovaries, with emphasis on the number of germinal beds. J. Herpetol. 16:240–252.

Licht, P. 1972. Environmental physiology of reptilian breeding cycles: Role of temperature. Gen. Comp. Endocrinol. Suppl. 3:477–488.

———. 1984. Reptiles. Pp. 206–282. *In* G. E. Lamming (Ed.), Marshall's Physiology of Reproduction, 4th Ed. Vol. 1: Reproductive Cycles of Vertebrates. Churchill Livingstone, Edinburgh.

Marion, K. R. 1982. Reproductive cues for gonadal development in temperate reptiles: Temperature and photoperiod effects on the testicular cycle of the lizard *Sceloporus undulatus*. Herpetologica 38:26–39.

Mendez de la Cruz, F. R., and M. Villagran Santa Cruz. 1983. Contribucion al conocimiento de la ecologia y ciclo reproductor de la lagartija vivipara *Sceloporus mucronatus mucronatus*. Biologia Tesis Profesional, U.N.A.M., Mexico City.

Miller, M. R. 1951. Some aspects of the life history of the yucca night lizard, *Xantusia vigilis*. Copeia 1951:114–120.

Ortega, A., and R. Barbault. 1984. Reproductive cycles in the mesquite lizard, *Sceloporus grammicus*. J. Herpetol. 18:168–175.

Stebbins, R. C. 1958. A new alligator lizard from the Panamint Mountains, Inyo County, California. Am. Mus. Novitates 1883:1–27.

Stewart, J. R. 1979. The balance between number and size of young in the live bearing lizard *Gerrhonotus coeruleus*. Herpetologica 35:342–350.

Stewart, J. R., and R. E. Castillo. 1984. Nutritional provision of the yolk of two species of viviparous reptiles. Physiol. Zool. 57:377–383.

Thompson, J. 1981. A study of the sources of nutrients for embryonic development in a viviparous lizard, *Sphenomorphus quoyii*. Comp. Biochem. Physiol. 70A:509–518.

———. 1982. Uptake of inorganic ions from the maternal circulation during development of the embryo of a viviparous lizard, *Sphenomorphus quoyii*. Comp. Biochem. Physiol. 71A:107–112.

Tinkle, D. W. 1972. The dynamics of a Utah population of *Sceloporus undulatus*. Herpetologica 28: 351–359.

Tinkle, D. W., and R. E. Ballinger. 1972. *Sceloporus undulatus*: A study of the intraspecific comparative demography of a lizard. Ecology 53: 570–584.

Tinkle, D. W., H. Wilbur, and S. Tiley. 1970. Evolutionary strategies in lizard reproduction. Evolution 24:55–74.

Vial, J. L., and J. R. Stewart. 1985. The reproductive cycle of *Barisia monticola*: A unique variation among viviparous lizards. Herpetologica 41: 51–57.

VINEGAR, M. B. 1975. Life history phenomena in two populations of the lizard *Sceloporus undulatus* in southwestern New Mexico. Am. Midl. Nat. 93:388–402.

VITT, L. 1973. Reproductive biology of the anguid lizard, *Gerrhonotus coeruleus principis*. Herpetologica 29:176–184.

WEEKES, H. C. 1935. A review of placentation among reptiles with particular regard to the function and evolution of the placenta. Proc. Zool. Soc. London 1935:625–645.

YARON, Z. 1977. Embryo-maternal interrelations in the lizard *Xantusia vigilis*. Pp. 271–277. *In* J. H. Calaby and C. H. Tyndale-Biscoe (Eds.), Reproduction and Evolution. Australian Acad. Sci., Canberra.

———. 1985. Reptilian placentation and gestation: Structure, function and endocrine control. Pp. 527–603. *In* C. Gans and F. Billett (Eds.), Biology of the Reptilia, Vol. 15: Development B. Wiley and Sons, New York.

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