

EVOLUTION OF VIVIPARITY IN THE LIZARD GENUS *SCELOPORUS*

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ABSTRACT: According to the cold-climate model, viviparity in squamate reptiles evolves at high elevations and latitudes. The lizard genus *Sceloporus* has been used to support this model; viviparous species are found at higher elevations than oviparous species. For example, in the *scularis* species group, a viviparous species replaces its oviparous sister species at elevations above 3000 m. We used recent literature to evaluate four aspects of the evolution of viviparity within the genus and concluded that (1) viviparity has evolved a minimum of four times within the genus. (2) Viviparity has not evolved at high latitudes, because the oviparous species found at high latitudes lack the morphological and physiological features that facilitate prolonged egg retention, the intermediate stage between oviparity and viviparity. (3) Viviparous species have not invaded high latitudes because viviparity in *Sceloporus* is associated with gestation during winter months. This is a viable reproductive mode at high elevations at tropical latitudes, because ambient temperatures during the winter are similar to those in the summer. At high latitudes, in contrast, winters may be too cold to support embryogenesis, or perhaps even survival of embryos. (4) Viviparity evolved from oviparity through three major transitions. The first was the evolution of viviparity from oviparity; this transition was associated with the invasion of high elevations. The second transition was a shift from summer to winter gestation such that birth was shifted from autumn to spring. With birth in the spring, neonates are able to mature by autumn, and consequently they can produce a litter within a year of their own birth. The third transition was a shift from asynchronous reproductive cycles of males and females (mating in spring and fertilization in autumn) to synchronous reproductive cycles (mating and fertilization in the autumn).

Key words: *Sceloporus*; Reproductive cycles; Evolution of viviparity

ABOUT 20% of the squamate reptiles are viviparous, and viviparity has evolved 100 or more times independently in this taxon (Blackburn, 1982; Shine, 1985). Because of the large number of origins, the power of comparative analyses can be applied to the question "what ecological features are associated with the evolution of viviparity?". Such analyses facilitate the rejection of hypotheses that relate viviparity to species characteristics such as arboreal or aquatic habitats and large size or strong defensive capabilities or that relate viviparity to habitat features such as aridity or excessive moisture (Shine, 1985). In contrast, comparative analyses provide strong support for the evolution of viviparity at high elevations and latitudes, that is, in cold climates (Shine, 1985). The benefit of

extended egg retention and viviparity in cold climates is thermal; because of the thermoregulatory capabilities of females, embryos in utero will be warmer than embryos in nests. Because embryonic development is temperature dependent, egg retention will enhance the rate of embryonic development or even the survival of embryos. One line of support for this hypothesis is the observation that viviparous species comprise a larger proportion of squamate faunas at high elevations or latitudes than at low elevations or latitudes (Packard et al., 1977; Tinkle and Gibbons, 1977; Weekes, 1935). Even more compelling support for this hypothesis is provided by the association between recent origins of viviparity and high elevations and latitudes (Guillette, 1982a; Qualls et al., 1995; Shine and Bull, 1979).

The geographic distribution of viviparity

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TABLE 1.—Species of *Sceloporus* whose modes of reproduction are known. Species groups and species are listed in the order in which they appear in Figs. 9–11 in Weins and Reeder (1997). Mode of reproduction: O = oviparous, V = viviparous. Unless otherwise noted, the source for reproductive mode in Guillette et al. (1980). While *S. cryptus* and *S. subpictus* were listed by Guillette et al. (1980) as oviparous, their sources (Lynch and Smith, 1965; Smith and Lynch, 1967) inferred the reproductive mode of these species from the reproductive mode of supposedly related species; we consider reproductive mode of these species to be unknown.

Group	Species	Reproductive mode
<i>variabilis</i>	<i>S. chrysostictus</i>	O
	<i>S. variabilis</i>	O
	<i>S. teapensis</i>	O
	<i>S. cozumelae</i>	O
	<i>S. couchii</i>	O
<i>utiformis</i>	<i>S. parvus</i>	O
	<i>S. utiformis</i>	O
	<i>S. siniferus</i>	O
<i>siniferus</i>	<i>S. carinatus</i>	O
	<i>S. squamosus</i>	O
	<i>S. merriami</i>	O
<i>maculosus</i>	<i>S. maculosus</i>	O
<i>gadoviae</i>	<i>S. gadoviae</i>	O
<i>jalapae</i>	<i>S. jalapae</i>	O
<i>pyrocephalus</i>	<i>S. ochoterenae</i>	O
	<i>S. nelsoni</i>	O
	<i>S. pyrocephalus</i>	O
<i>graciosus</i>	<i>S. graciosus</i>	O
<i>scalaris</i>	<i>S. subniger</i> [*]	O
	<i>S. aeneus</i>	O
	<i>S. scalaris</i>	O
<i>megalepidurus</i>	<i>S. bicanthalis</i>	V
	<i>S. goldmani</i> ^{**}	V
	<i>S. chaueyi</i> ^{***}	O
	<i>S. megalepidurus</i> ^{****}	V
	<i>S. dugesii</i>	V
	<i>S. bulleri</i>	V
	<i>S. torquatus</i>	V
	<i>S. insignis</i>	V
	<i>S. prezygus</i>	V
	<i>S. serrifer</i>	V
	<i>S. jarrovi</i>	V
	<i>S. macdougalli</i>	V
	<i>S. mucronatus</i>	V
	<i>S. poinsettii</i>	V
	<i>S. cyanogenys</i>	V
<i>grammicus</i>	<i>S. ornatus</i>	V
	<i>S. grammicus</i>	V
	<i>S. asper</i>	V
	<i>S. heterolepis</i>	V
	<i>S. shannonorum</i>	V
<i>undulatus</i>	<i>S. palaciosi</i> ^{*****}	V
	<i>S. undulatus</i>	O
	<i>S. woodi</i>	O
	<i>S. occidentalis</i>	O
	<i>S. virgatus</i>	O
	<i>S. exul</i>	O
	<i>S. cautus</i>	O

TABLE 1.—Continued.

Group	Species	Reproductive mode
<i>olivaceus</i>	<i>S. olivaceus</i>	O
<i>spinosus</i>	<i>S. spinosus</i> ^{*****}	O
	<i>S. horridus</i>	O
	<i>S. rufidorsum</i>	O
<i>formosus</i>	<i>S. formosus</i>	V
	<i>S. adleri</i>	V
	<i>S. stejnegeri</i>	V
	<i>S. tanneri</i>	V
	<i>S. malachiticus</i>	V
	<i>S. acanthinus</i>	V
	<i>S. lunaei</i>	V
	<i>S. internasalis</i>	V
	<i>S. taeniatus</i>	V
	<i>S. hundertli</i>	O
<i>edwardtaylori</i>	<i>S. edwardtaylori</i>	O
<i>clarkii</i>	<i>S. clarkii</i>	O
<i>magister</i>	<i>S. melanorhinus</i>	O
	<i>S. magister</i>	O
	<i>S. orcutti</i>	O
	<i>S. hunsakeri</i>	O
	<i>S. lieki</i>	O

* Poglayen and Smith (1958) and Smith et al. (1993) considered that *subniger* refers to *S. aeneus subniger*. Populations of this subspecies are found at the base of Nevado de Toluca and, like other populations of *S. aeneus*, are oviparous. The viviparous populations of the *scalaris* group found at elevations of approximately 3000 m or higher on Nevado de Toluca represent *S. bicanthalis*.

** Mink and Sites (1996).

*** Mink and Sites (1996).

**** Godínez-Cano (1985).

***** Méndez-de la Cruz (1989).

***** Martínez-Lova (1998).

in the lizard genus *Sceloporus* supports the cold climate model. In this genus of approximately 70 species, approximately 30 are viviparous (Sites et al., 1992). The number of viviparous species relative to the total number of species of *Sceloporus* increases with elevation, and viviparity is the dominant mode of reproduction at >1500 m (Guillette et al., 1980). Moreover, the genus includes at least one example of a recent origin of viviparity that is associated with high elevation (Guillette, 1982a). The viviparous *Sceloporus bicanthalis* replaces its close relative *Sceloporus aeneus* on an elevation gradient in the transvolcanic axis of central Mexico; *S. aeneus* is found up to elevations of approximately 3000 m and *S. bicanthalis* is found from approximately 2000 m to >4000 m (Benabib et al., 1997; Camarillo, 1990).

Since Guillette et al. (1980) discussed the evolution of viviparity in *Sceloporus*, considerably more information on the bi-

ology and phylogenetic relationships of *Sceloporus* have become available. We use this information to evaluate four questions. (1) How many times did viviparity evolve in the genus *Sceloporus*? (2) Why have viviparous species of *Sceloporus* not evolved at high latitudes, even though the range of the genus extends into the state of Washington, U.S.A? (3) Why does the range of viviparous species of *Sceloporus* extend only as far north as southern Arizona whereas the ranges of other viviparous taxa (e.g., *Thamnophis sirtalis*) extend into Canada? (4) Why is the shift from oviparity to viviparity in *Sceloporus* associated with shifts in the seasonal pattern of reproduction, and how did these shifts come about?

MULTIPLE ORIGINS OF VIVIPARITY

Viviparity occurs in five species groups (sensu Weins and Reeder, 1997) (Table 1); it is apparently fixed in the *formosus*, *grammicus*, *torquatus*, and *megalepidurus* groups, whereas the *scalaris* group contains both oviparous and viviparous species. The observation by Godínez-Cano (1985) that *S. megalepidurus* is actually viviparous, and not oviparous as previously designated (Guillette et al., 1980), resolves a problem posed by Sites et al. (1992). This problem is the possible reversion to oviparity from viviparity that may have occurred if *S. megalepidurus* were oviparous, given its close relationship to the *grammicus* and *torquatus* groups. However, the more recent analyses of Weins and Reeder (1997) suggest that viviparity arose once in a common ancestor of these lineages, rather than on three separate occasions (Fig. 1). The *scalaris* group includes two viviparous species, and viviparity apparently has had two (Benabib et al., 1997; Mink and Sites, 1996) origins in this group. Overall, viviparity has arisen a minimum of four times in the genus *Sceloporus*, once in the *formosus* group, once in the lineage including the *grammicus*, *torquatus*, and *megalepidurus* groups, and twice in the *scalaris* group.

Recent suggestions of reversals of viviparity to oviparity (Nopalillo population) or of reproductive bimodality (Las Vigas

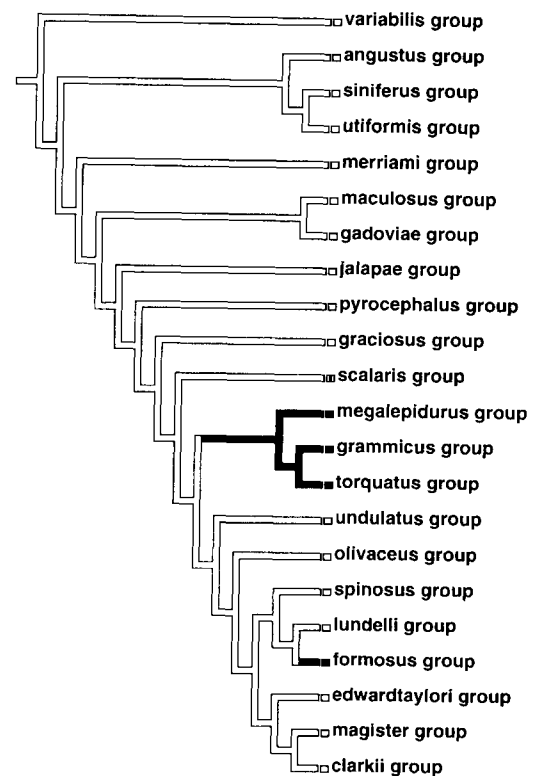


FIG. 1.—Relationships among the species groups of *Sceloporus* following Weins and Reeder (1997). Open bars represent oviparity and solid bars represent viviparity. Only the *scalaris* species group has both oviparous and viviparous members. Origins of viviparity were determined from the character tracing section of the MacClade 3.02 phylogenetic program (Maddison and Maddison, 1992). Results using the Equivocal Cycling, Deltran, and Actran options were identical.

population) in the *S. bicanthalis* complex (Benabib et al., 1997; Creer et al., 1997; Mink and Sites, 1996), although tantalizing, seem to be premature. The reproductive condition of voucher specimens of *S. bicanthalis* deposited in the Museum of Zoology at the Facultad de Ciencias, Universidad Nacional Autónoma de México and in the Monte L. Bean Life Science Museum, Brigham Young University, from the Nopalillo and Las Vigas sites of Mink and Sites (1996) was re-examined by one of us (M. Villagrán). Reproductive females were either vitellogenic or contained recently ovulated eggs (embryos too small to stage). These specimens cannot be used to

evaluate reproductive mode because they could be either oviparous or viviparous (Blackburn, 1993). More importantly, subsequent collections of females of *S. bicanthalis* from these two sites, have all proven to be viviparous (laboratory observations of F. Méndez and M. Villagrán, personal communication of Miriam Benabib). The presence of oviparous *S. bicanthalis* at the Nopalillo and Las Vigas sites has thus not been confirmed.

DISTRIBUTION OF VIVIPARITY RELATIVE TO LATITUDE AND ELEVATION

Viviparous species of *Sceloporus* are found from western Panama in Central America to southern Arizona, New Mexico, and Texas in the United States. The highest number of viviparous species, 13, is found between 18° and 20° north latitude (data from range maps of Sites et al., 1992). Viviparity in this genus is thus strongly associated with the high mountains of the Transvolcanic axis of Central Mexico. In contrast, while the range of oviparous species extends into Costa Rica, almost as far south as viviparous species, the range of oviparous species extends north almost to the Canadian border of the United States, at 49° north latitude. The range of viviparous species is thus almost completely restricted to tropical latitudes whereas the range of oviparous species extends far into temperate latitudes.

The observation that viviparous species of *Sceloporus* do not occur at high latitudes has two components. The first is why viviparity has not evolved at high latitudes. Guillelte et al. (1980) suggested that "selective pressures associated with high latitude have not resulted in a preponderance of placental viviparous species because embryos of high latitude, egg retaining females do not suffer gas diffusion problems as much as do those at high altitudes." While this explanation could be correct for *Sceloporus*, it is not in accord with the occurrence of viviparous species at high latitudes in many other squamate taxa (Shine, 1985). At least two alternative explanations are more plausible. One is that the selective pressures at high latitudes are not the same as those at high elevations at

low latitudes. For example, cold temperature per se may not favor the transition to viviparity unless associated with particular seasonal changes in temperature, moisture, or food availability.

Another explanation for the absence of viviparous species at high latitudes is that the particular groups of oviparous *Sceloporus* that invaded high latitudes of North America did not have morphological or physiological features that would facilitate the evolution of viviparity. For example, *S. occidentalis*, the species with the northernmost range, is a member of the *undulatus* species group. Most members of this group lay eggs at approximately stage 30 (hatching or birth occurs at stage 40: stages of Dufaure and Hubert, 1961) regardless of environmental conditions (T. Mathies, personal communication; Sexton and Marion, 1974). Moreover, even though females of *S. virgatus* can support embryonic development in utero past stage 30, embryonic development is retarded (Andrews and Rose, 1994). Successful egg retention beyond stage 30, the transitional stage between oviparity and viviparity, is thus not observed in the *undulatus* group. Extension of egg retention that does not impair embryonic development has thus far been observed only in the *scularis* group (Mathies and Andrews, 1995, 1996), and this is the only group within *Sceloporus* with a comparatively recent evolution of viviparity.

The other component to the observation that viviparous species of *Sceloporus* do not occur at high latitudes is why viviparous species have not extended their ranges further into North America. We suggest that the particular reproductive phenology associated with viviparity in *Sceloporus* is ecologically incompatible with reproductive success at high latitudes. All viviparous species of *Sceloporus* except *S. bicanthalis* ovulate in the autumn and gestation continues over the winter. At tropical latitudes, "winter" is not particularly cold; the mean temperature of the coldest and warmest month of the year differs by only a few degrees at all elevations (Janzen, 1967), and lizards are active year round. The difference between summer and win-

ter temperatures increases with latitude, and most temperate zone lizards hibernate during the winter. The northern limits of viviparous species of *Sceloporus* (southern Arizona, New Mexico, and Texas) may thus coincide with climates mild enough for pregnant females to bask, at least occasionally, during the winter (Ruby, 1977). At even more northerly latitudes, low body temperatures of hibernating females may preclude development, or even survival, of embryos over the winter.

A thermal limit to the northward invasion of viviparous species of *Sceloporus* is supported by observations on the reproductive cycles of other viviparous lizard taxa in North America. For example, the ranges of the viviparous *Phrynosoma douglassi* and *Gerrhonotus coeruleus* extend into Canada. Unlike *Sceloporus*, however, viviparous females of these species are not pregnant over the winter months; gestation occurs during summer, and birth occurs in the autumn.

EVOLUTION OF REPRODUCTIVE CYCLES

Oviparous and viviparous species of *Sceloporus* exhibit different seasonal patterns of reproduction. The reproductive activity of all oviparous species is restricted to spring and summer, and this temporal span is independent of latitude. For example, the oviparous *S. acneus* at 19° N, *S. scalaris* at 32° N, and *S. occidentalis* and *S. graciosus* at 34° N latitude all exhibit essentially the same reproductive phenology. Vitellogenesis is initiated in the spring, oviposition of one or more clutches occurs during late spring and summer, and eggs hatch in late summer and autumn (Fig. 2A). At temperate latitudes, the time of reproductive activity corresponds to the warm season, whereas at tropical latitudes, where seasonality reflects the alternation of wet (summer) and dry (winter) seasons, the period of reproductive activity corresponds to the wet season. At both temperate and tropical latitudes, however, reproductive activity is associated with the time of most abundant food resources for lizards (Levings and Windsor, 1982; Méndez-de la Cruz et al., 1992).

In contrast, for all viviparous species of

Sceloporus except *S. bicanthalis* (see below), vitellogenesis is initiated in late summer or autumn, gestation continues throughout the winter, and parturition occurs in spring (Figs. 2C,D). Females of viviparous species are actually reproductive (vitellogenic or pregnant) during 9–10 mo of the year! The long reproductive cycle of viviparous species is related, in part, to their high elevation habitats where mean body temperatures of females are relatively low (Andrews et al., 1997; Andrews et al., unpublished data). The consequence of reduced rates of vitellogenesis and embryonic development at low temperatures (e.g., Muth, 1980) is that the reproductive cycle is protracted at high elevations; all viviparous species of *Sceloporus* are single-brooded. This seasonal pattern of reproduction is also characteristic of other viviparous squamate taxa at high elevations in Mexico (Guillette, 1982b; Guillette and Casas-Andreu, 1987).

The evolution of viviparity in the genus *Sceloporus* is thus associated with a major shift in the phenology of reproduction. We suggest that the main selective force behind the shift in the period of gestation from summer to winter is that birth for viviparous species occurs in the spring. Birth in the spring provides two related benefits. One benefit is that birth occurs at the beginning of the wet season, when food for neonates is most abundant and ambient temperatures are relatively high (Méndez-de la Cruz et al., 1992). The second, and related benefit, is that neonates at tropical latitudes are able to reach sexual maturity and mate in the autumn following birth (González-Ruiz, 1991; Guillette and Méndez-de la Cruz, 1993; Méndez-de la Cruz et al., 1995). Age at first reproduction affects the intrinsic rate of increase more than the total number of progeny (Cole, 1954); early reproduction would thus compensate viviparous females, at least in part, for the reduction in numbers of clutches produced per year (≥ 1 for oviparous species and one for viviparous species). In southern Arizona, where relatively cold winters reduce growth rates of embryos in utero, the reproductive cycle of viviparous species may

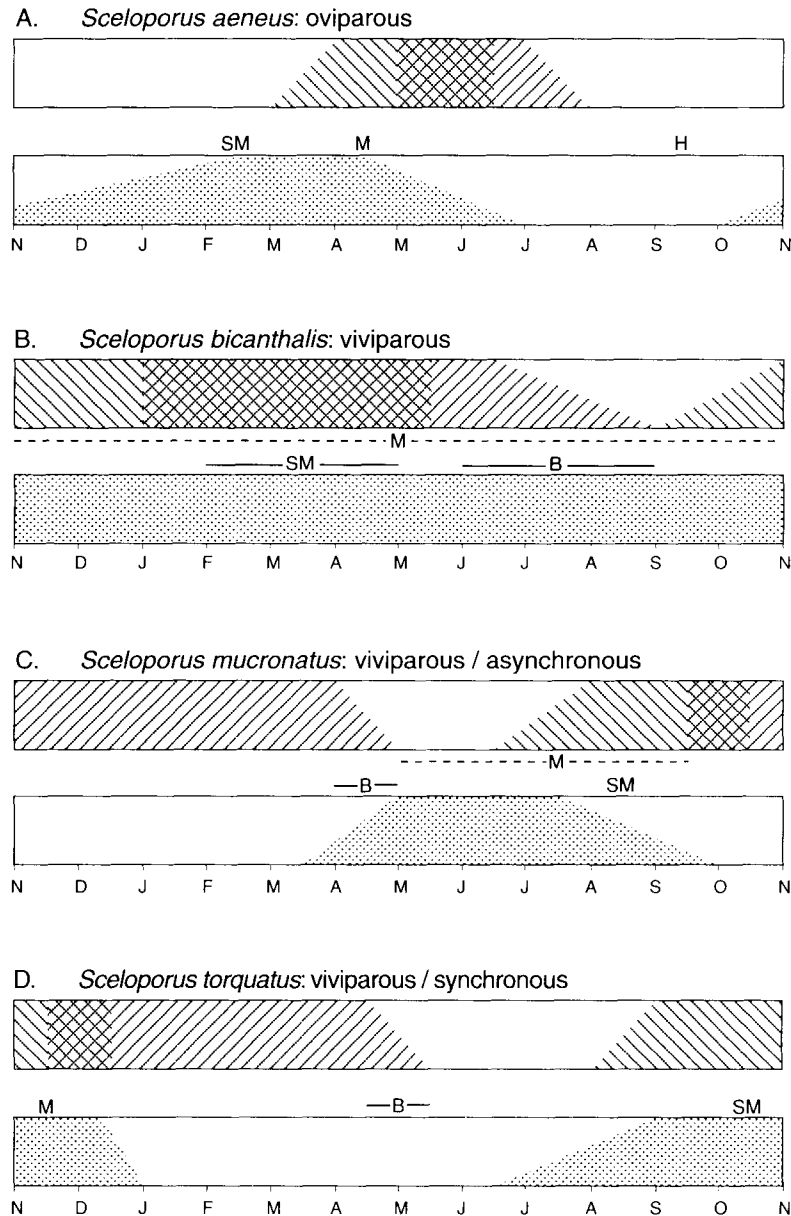


FIG. 2.—Reproductive patterns of (A) *Sceloporus aeneus*, oviparous (Guillette, 1982a; Manríquez-Morán, 1995), (B) *Sceloporus bicanthalis*, viviparous (Guillette, 1982a; Hernández-Gallegos, 1995; Manríquez-Morán, 1995), (C) *Sceloporus mucronatus*, viviparous/asynchronous (Méndez-de la Cruz et al., 1988), and (D) *Sceloporus torquatus*, viviparous/synchronous (Guillette and Méndez-de la Cruz, 1993). For each species, the reproductive cycles of females and males are represented by the upper and lower boxes respectively. For females, hatched areas represent the proportions of adult females that are reproductive; vitellogenesis is represented by back slashed hatching, gravidity or gestation is represented by forward slashed hatching, and the period of ovulation is represented by cross-hatching. For males, the stippled area represents the relative size of the testes. H, B, SM, and M indicate times of hatching, birth, attainment of sexual maturity, and mating, respectively.

be even more protracted. For example, 60% of female neonates in *S. jarrovi* at 1700 m matured and mated during their first autumn, and at a higher elevation (2500 m), maturity of all neonates was delayed to the following year (Ballinger, 1973).

Almost all viviparous squamates produce only one clutch per year, and this reproductive mode is often associated with relatively large body size and delayed maturity (Dunham et al., 1988). These latter traits presumably provide compensation in terms of enhanced survival for the low reproductive output of viviparous species. In *Sceloporus*, however, this potential handicap of viviparity has been overcome by precocious maturity; females produce their first litters within a year of their own birth. Dunham et al. (1988) pointed out that females of *S. jarrovi* were particularly early maturing within viviparous lizards in general; our observations on other species of *Sceloporus* suggest that early maturity may be associated with the evolution of viviparity in this genus.

EVOLUTION OF THE FEMALE REPRODUCTIVE CYCLE IN VIVIPAROUS SPECIES

How does the shift from oviparity to viviparity occur? Clues to this phenomenon may be found in the reproductive biology of members of the *scalaris* species group. The pivotal species are *S. aeneus* and *S. bicanthalis*. These closely related species (Benabib et al., 1997; Mink and Sites, 1996) replace each other on an elevational gradient (Camarillo, 1990); we assume that viviparity evolved in those places where the viviparous *S. bicanthalis* now occurs. The reproductive cycle of *S. aeneus* is typical of that of oviparous species of *Sceloporus*; reproduction is initiated in the spring and hatching occurs in the autumn (Fig. 2A). In contrast, for *S. bicanthalis*, vitellogenesis commences in the autumn (Fig. 2B). Ovulation occurs as early as January and pregnant females are found through the summer, with most births concentrated in summer and autumn (Guillette, 1982a; Manríquez-Morán, 1995). The reproductive cycles of individual females are

not well synchronized so that there is considerable overlap in reproductive classes (non-reproductive, vitellogenic, pregnant). For example, at least a few pregnant females can be found from January through September (Manríquez-Morán, 1995). Despite the comparatively weak reproductive seasonality exhibited by *S. bicanthalis*, the coincidence of the period of hatching for *S. aeneus* and birth for *S. bicanthalis* suggests that the transition from oviparity to viviparity was associated with early initiation of the reproductive cycle in populations of the oviparous ancestor of *S. bicanthalis* (Fig. 2A vs. 2B). A shift to earlier vitellogenesis and a longer period of egg retention at high elevations would have maintained hatching (or birth) in the autumn.

The *S. bicanthalis* model is supported by observations on the oviparous lizard *Sceloporus scalaris* in Arizona; females from high elevation populations initiate vitellogenesis and ovulation earlier in the spring and retain eggs longer than females from low elevation populations (Mathies and Andrews, 1995). Cooler temperatures are thus associated with a protracted reproductive season for high elevation populations. Nonetheless, because of the earlier initiation of reproduction at high than low elevations, hatching in both populations of *S. scalaris* occurs about the same time in the autumn. Presumably, the early initiation of reproduction by females from high elevation populations of *S. scalaris* compensates for relatively low body temperatures of females and correspondingly slowed embryonic development at high elevations. Similarly, the increasingly earlier initiation of reproduction and a continued increase in the length of egg retention as the oviparous ancestor of *S. bicanthalis* invaded higher and higher elevations would produce the reproductive pattern seen today. An important difference between Mexico and Arizona is, however, that mean daily temperatures of winter and summer months at high elevations in Mexico differ only by a few degrees, and winter is not a thermal barrier to vitellogenesis and gestation.

Assuming that *S. bicanthalis* represents

TABLE 2.—Reproductive cycles of viviparous species of *Sceloporus*. Oviparous species are not listed because they all have synchronous reproductive cycles. Mode = viviparous and asynchronous (V/A) or viviparous and synchronous (V/S) reproductive cycles (see text for details). Latitude (°N) and altitude (m) are for the referenced study populations.

Group	Species	Mode	Latitude	Altitude (m)	Reference
<i>formosus</i>	<i>S. formosus</i>	V/A	17–20°	~1600	Guillette and Sullivan (1985)
	<i>S. malachiticus</i>	V/A	10°	800–3200	Marion and Sexton (1971)
<i>grammicus</i>	<i>S. grammicus</i>	V/S	26°	50	Guillette and Bearce (1986)
		V/S	24°	2480	Ortega and Barbanlt (1984)
		V/S	19°	2500	Martínez-Isac (1985)
		V/A	19°	3200	Martínez-Isac (1985)
		V/A	19°	3200	Guillette and Casas-Andren (1980)
		V/A	19°	3200–3400	Méndez-de la Cruz (1989)
<i>scalaris</i>	<i>S. bicanthalis</i>	V/S	19°	3000–3850	Guillette (1982a)
		V/S	19°	3200	Mauriquez-Moran (1995);
					Hernández-Gallegos (1995)
<i>torquatus</i>	<i>S. torquatus</i>	V/S	19°	2250–2350	Feria-Ortiz (1986)
		V/S	19°	2600	Guillette and Méndez-de la Cruz (1993)
	<i>S. cyanogenys</i>	V/S	30°	~1000	Crisp (1964)
	<i>S. jarrovi</i>	V/S	32°	1520–2134	Goldberg (1971)
		V/S	32°	1825	Ruby (1977)
	<i>S. mucronatus</i>	V/S	32°	1980–2150	Guillette et al. (1981)
		V/S	32°	1675–2500	Ballinger (1973)
		V/S	19°	2600	Méndez-de la Cruz et al. (1994)
		V/A	19°	3200–3400	Méndez-de la Cruz et al. (1988)
	<i>S. poinsetti</i>	V/S	32°	1000	Ballinger (1973)
<i>megalepidurus</i>	<i>S. dugesi</i>	V/S	19°	2040	González-Rul Espinosa (1987)
	<i>S. megalepidurus</i>	V/S	19°	2500	Godínez-Cano (1985)

an intermediate stage in the evolution of viviparity, the further transition to the reproductive cycles typical of viviparous species would involve the shift from birth in the summer and autumn to birth in the spring (Fig. 2B vs. 2C and 2D). As we pointed out earlier, the selective benefit of this reproductive pattern is that neonates are able to grow to adult size by autumn (Figs. 2C,D).

ORIGIN OF ASYNCHRONOUS AND SYNCHRONOUS REPRODUCTION

For viviparous species, the reproductive cycles of females and males of a given species or population can be asynchronous or synchronous. When reproduction is asynchronous (*S. formosus*, *S. malachiticus*, and some populations of *S. grammicus* and *S. mucronatus*), testicular mass, and presumably the number of mature sperm, is greatest in the spring, mating presumably occurs at this time, and females store sperm until ovulation in autumn or winter (Table 2, Fig. 2C). Mating thus occurs well before fertilization. For species or populations with synchronous reproduction (*S.*

cyanogenys, *S. dugesi*, *S. jarrovi*, *S. megalepidurus*, *S. poinsetti*, *S. torquatus*, and some populations of *S. grammicus* and *S. mucronatus*), testicular mass, and presumably number of mature sperm is greatest in the autumn, and mating and fertilization coincide (Table 2, Fig. 2D).

We suggest that asynchronous mating was associated with the initial stages of the evolution of viviparity in high elevation habitats, and that synchronous mating was a later consequence of the invasion of lower and more arid habitats. In support, asynchronous reproduction is characteristic of populations of *S. grammicus* and *S. mucronatus* at 3000 m or more whereas conspecific populations <3000 m exhibit synchronous reproduction (Table 2). Selection on females for earlier and earlier vitellogenesis and ovulation (moved back from spring to autumn or winter) and an increase in the length of egg retention may not have affected the gonadal cycle of males, at least initially; mating would still have occurred in the spring, but with postpartum rather than with late vitellogenic females.

The above scenario is complicated by the timing of maturation of juvenile females. All females of *S. grammicus* from an asynchronous population at Parque Zoqueapan (3200 m) are pregnant in November (Cuellar et al., 1996). Females that would have been adults in June and July presumably mate at that time and store sperm until November when ovulation and fertilization occur (Villagrán-Santa Cruz et al., 1992). Females born in June and July, however, have sperm in their reproductive tracts by October (Villagrán-Santa Cruz, unpublished data). This means that the reproductive activities of males must extend into late summer and autumn. Perhaps testicular maturation and mating by males become at least partially disassociated (e.g., Crews, 1985) so that males are able to inseminate mature post-partum females in June and July and to inseminate newly mature females in the autumn.

Synchronous reproduction, in which gonadal activity of both sexes occurs in the autumn, is associated with populations or species at low to intermediate elevations (Table 2). Observations on two species with wide elevational ranges in Mexico suggest that the shift from high to low elevation habitats was associated with the shift from mating in the spring to mating in autumn. Populations of both *S. grammicus* and *S. mucronatus* at 3000 m or higher have asynchronous reproduction and populations <3000 m have synchronous reproduction. For these species, the shift in the time of testicular maturation may have occurred when climatic conditions became more arid and the oak-savannah forests of the Central Plateau were replaced by more xeric vegetation types in the Pleistocene (Martin, 1958). Males of high elevation (asynchronous) populations currently appear to be reproductively active from spring, when they mate with one year and older females, to autumn, when they mate with newly matured females. As a consequence of the more xeric conditions and relatively low food availability now prevalent at low elevations (Méndez-de la Cruz et al., 1994), selection may have favored males with a delayed onset of reproductive activity, and the concentration

of reproduction in the autumn when all females would be receptive rather than the energetically more costly protracted reproductive season of males at high elevations.

SUMMARY: EVOLUTION OF REPRODUCTIVE CYCLES

Viviparity in the genus *Sceloporus* involves three evolutionary transitions. The first is the transition of oviparity to viviparity. Species in the *scalaris* group provide a model for this transition. The reproductive cycles of the oviparous *S. aeneus* and the viviparous *S. bicanthalis* differ primarily in the degree of synchrony among individuals and in when vitellogenesis is initiated. Reproduction in populations of *S. bicanthalis* is much less synchronized (and males show no seasonal pattern at all) than in populations of *S. aeneus*. Vitellogenic females in populations of *S. bicanthalis* increase in frequency starting in January while vitellogenesis is initiated in March in populations of *S. aeneus*. The earlier initiation of reproduction of *S. bicanthalis* compensates for lower ambient temperatures, and, as a consequence, peak of hatching and birth for the two species occurs in the autumn. Presumably, the shift to earlier reproduction by the oviparous ancestor of *S. bicanthalis* was associated with an increase in the length of egg retention and, ultimately, viviparity.

The second evolutionary transition was from viviparity with birth in the autumn to viviparity with birth in the spring; that is, a shift in the female reproductive cycle from summer to winter gestation. Birth in the spring provides an important benefit; neonates are born at the time of maximum food abundance and relatively high ambient temperatures. As a consequence, neonates become sexually mature within months of birth. A parallel shift from summer to winter gestation has occurred in two other families of Mexican lizards [*Barisia* in the Anguidae (Guillette and Casas-Andreu, 1987) and *Eumeces* in the Scincidae (Guillette, 1982b)], suggesting that the selective forces acting on *Sceloporus* affected other taxa as well.

The third evolutionary transition was

from viviparity with asynchronous reproductive cycles of males and females to viviparity with synchronous cycles of males and females. Asynchronous reproduction for males apparently involves continuous reproductive activity from spring to autumn, which accommodates receptivity of old females in the spring and newly matured females in the autumn. Synchronous reproductive cycles are associated with low to moderate elevation habitats that are less productive than the high elevation habitats where viviparity evolved. Synchrony of males and females such that mating occurred in the autumn may thus have resulted from selection for a shorter period of male reproductive activity.

RESUMEN

De acuerdo con el modelo del clima frío, la viviparidad en reptiles escamosos ha evolucionado en elevaciones y latitudes altas. Las lagartijas del género *Sceloporus* han sido utilizadas para apoyar este modelo ya que las especies vivíparas se encuentran en lugares más elevados que las ovíparas. Por ejemplo, en el grupo *scalaris* una especie ovípara es reemplazada por su especie hermana vivípara en elevaciones mayores de 3000 m. Utilizamos la literatura reciente para evaluar cuatro aspectos de la evolución de la viviparidad dentro del género y concluimos que (1) La viviparidad ha evolucionado por lo menos cuatro veces. (2) La viviparidad no ha evolucionado en latitudes boreales por que las especies que las habitan carecen de las características morfológicas y fisiológicas que facilitan la retención prolongada del huevo, lo cual es el estadio intermedio entre la oviparidad y la viviparidad. (3) Las especies vivíparas no han invadido las latitudes boreales por que la viviparidad en *Sceloporus* esta asociada con la gestación durante el invierno. Este es un tipo de reproducción viable en elevaciones altas a latitudes tropicales debido a que en estos sitios las temperaturas de invierno y verano son similares. En latitudes boreales los inviernos son demasiado fríos para permitir la embriogénesis e incluso quizá para la sobrevivencia de los embriones. (4) La viviparidad evolucionó de la oviparidad a

través de tres grandes cambios. El primero fue la evolución de la oviparidad a la viviparidad; este cambio estuvo asociado con la invasión a las elevaciones altas. El segundo fue el cambio de la gestación del verano al invierno, de tal manera que el nacimiento pasó del otoño a la primavera. Con el nacimiento en primavera, los neonatos pudieron madurar en el otoño y consecuentemente producir una camada dentro del primer año de vida. El tercero fue el cambio de los ciclos reproductores asincrónicos de machos y hembras (apareamiento en la primavera y fertilización en el otoño) a los ciclos reproductores sincrónicos (apareamiento y fertilización en el otoño).

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