The Distribution and Evolution of Viviparity in Reptiles

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INTRODUCTION

Live-bearing habits (used synonymously with viviparity in this paper), while exhibited by only 15 per cent or less of the world's species of reptiles, are nevertheless geographically widespread and have arisen independently in many different reptile families. Several hypotheses have been put forth to explain the selective pressures that lead to viviparity in reptiles. One of these, by virtue of its simplicity and the fact that it has been oft repeated, has gained the status of conventional wisdom. This is the hypothesis that viviparity is an adaptation to a cold climate.

Our purpose is to review thoroughly the evidence supporting the cold adaptation hypothesis, as well as other less general hypotheses proposed by various authors, to determine to what extent the available data support them. The literature on viviparous reptiles has never been thoroughly reviewed; thus, it is difficult to support or refute any particular hypothesis. In addition, we review the life history phenomena of egg-retention and egg-guarding which appear to be related directly or indirectly to the evolution of viviparity. Finally, we offer new hypotheses for the evolutionary significance of viviparity in reptiles. It should be recognized from the outset that both oviparous and viviparous modes of reproduction have disadvantages as well as advantages associated with them (Table 1), so that the relative importance of each of these must be ascertained to determine which

TABLE 1
POSSIBLE BENEFITS OF DIFFERENT REPRODUCTIVE MODES AMONG REPTILES

OVIPARITY	VIVIPARITY
Parent not encumbered by enlarged eggs or embryos for prolonged periods so that risk and maintenance costs are lower	Protection of eggs from some environmental sources of mortality
	Favorable thermoregulation of developing embryos
Multiple clutches more likely	
	Female can add sustenance during development rather than making the entire reproductive commitment at the time of ovulation
Eggs separate from female in event of adult mortality	
Higher probability of genetic diversity among offspring as a result of multiple matings and multiple clutches	Greater predictability in placement of newborn young in sites optimal for them

reproductive mode will prevail in a particular case. We would also like
to call attention to the fact that reproductive mode is still unknown
for many of the world's squamates and future workers are urged to
collect this basic information.

Review of Ideas and Evidence Concerning Viviparity in Reptiles

Weekes (1935) is generally credited with the idea that viviparity
is an adaptation to cold environments. She showed that the majority
of lizards at high elevations in Australia are viviparous. Nevertheless,
very similar, if not identical, ideas were expressed earlier by Gadow
(1910), whose studies of Mexican amphibians and reptiles indicated
that most reptiles living above 10,000 feet in elevation are viviparous.
Similarly, Mell (1929) noted in his studies of Chinese reptiles that
viviparity is particularly common among species at localities in the
north or at high altitudes. However, the first and still the best
quantitative study was that of Sergeev (1940) on the distribution of
viviparity in reptiles, principally in Eurasia. He showed clearly that
the percentage of viviparous species is greatest at high latitudes and
high elevations. In his words (translation): "It is incontrovertible that
for lizards, snakes and all reptiles combined there is an increase in
percentage of viviparous species from south to north. In fact, in the
most northerly areas, almost all species are viviparous." Sergeev
(1940) also provided a clear explanation for the selective pressures
which he thought favor the evolution of viviparity: "The eggs laid in
a cold locality in the soil have to be developed at cold temperatures.
As a result, development is long term with a higher likelihood of
death from predators, drought, etc. Also, eggs may not have time to
complete development in the warm season. A viviparous female on
the other hand can bask by day and seek burrows by night and thus
control temperature of the embryos nearer the optimum for develop-
ment." Packard (1966) presented essentially the same idea, but with
more detailed explanations of the intermediate stages in the evolution
of viviparity from oviparity.
  That this idea has been widely accepted is indicated by quota-
tions from general texts, semi-popular literature, and professional
journals. Thus, Greer (1966) stated that "The correlation between life
in the cooler climates of higher altitudes and latitudes, and viviparity
(including so-called ovoviviparity) in the Squamata is generally well
known to herpetologists." Robb (1973) noted "There is a definite
adaptive significance in viviparity for lizards living in cool cli-
mates . . . " Goin and Goin (1971) suggested that "Snakes and lizards
that live at high altitudes or latitudes typically bear living young."
Porter (1972) stated that: "As with lizards, there is often a correla-
tion between viviparity in snakes and occupation of cool high altitude
or high latitude habitats." Neill (1964) in his thoughtful review of
viviparity in snakes also noted the evidence for an association

between high latitudes, high altitudes and viviparity but suggested several other interesting correlations (as did Mell, 1929) which will be discussed later. While the authors cited above primarily call attention to the correlation between viviparity and cold climates, causation is clearly implicit, and is explicit in the previous quotation from Sergeev (1940).

Nevertheless, some authors have not been convinced of a causal relationship between cold environments and viviparity. Thus, Kopstein (1938), who studied the reptiles of Java, commented that "The reason of viviparity is not known. We find in apparently the same biological circumstances, in the same biotop oviparous and (ovo-) viviparous forms living next to each other. The geographical altitude, temperature and humidity certainly play no part and the explanation may rather be phylogenetical." Bauchot (1965) emphasized that "Viviparity is a widespread phenomenon not explainable by climatic condition." Tinkle (1967) stated: "I might suggest that viviparous species are the ones that can take advantage of such situations (cold and dry conditions), but the evolution of viviparity may, in reality, be unrelated to them."

Because many authors have emphasized the adaptive significance of viviparity we feel it necessary to point out that viviparity has certain potential, if not automatic, disadvantages associated with it. Because of these, the circumstances under which its evolution will be favored by selection may be quite restricted, thereby placing the relative rarity of this reproductive mode in reptiles in perspective. Some of the disadvantages of viviparity are (also see Table 1 for a list of advantages):

1. Fecundity of a viviparous female would be potentially lower than that of an egg-laying female in the same population owing to her long period of intra-uterine embryonic development, if the egg-laying female were able to produce several clutches in the same period of time. It might be objected that the viviparous female could simply produce the same number of young, but at one period. This, however, could entail a high risk to the parent inasmuch as these young would constitute a high proportion of her total body weight.

      We recognize that in actuality it is unlikely that reproductive modes as different as viviparity and multiple-brooded oviparity would exist simultaneously in the same population. What we are stressing is the potential reduction in fecundity that would accompany a transition from multiple-broodedness to viviparity.

2. The death of the female during the gestation period would result in the loss of her offspring. An egg-laying parent is separated from her young during most of their period of development; therefore her own death will not affect the survival of her offspring.

3. Viviparous species may be less able than oviparous ones to
    maximize genotypic diversity among their offspring. This is
    because fewer litters in each season, relative to multiple-
    clutched oviparous species, reduce the probable number of
    different males with which each viviparous female mates, as
    well as restricting the total number of her offspring. We
    consider this the least important disadvantage of being vivi-
    parous and will not discuss it further (see Williams, 1975).

In the sections that follow, we present data on the correlation
of latitude and altitude with viviparity in several well-studied herpeto-
faunas in different parts of the world, data on the distribution of
viviparity across taxonomic groups of reptiles, data on incubation and
gestation periods, and data on extent of embryonic development
prior to egg deposition in oviparous species. With such information
we attempt to answer the following questions:

1. Is there convincing evidence for a causal as well as a
    correlative relationship between cold environments and the
    evolution of viviparity? With what independent variables
    other than cold environments is viviparity correlated?
2. Is there evidence that viviparity, once evolved in a taxon, is
    irreversible, such that some instances of viviparity represent
    phylogenetic constraint? Are there instances in which ovi-
    parity and viviparity occur in the same species in different
    parts of the range?
3. Are embryonic developmental times generally shorter for
    viviparous species than for oviparous ones, and do they vary
    geographically?
4. Are intermediate stages identifiable in the transition from
    oviparity to viviparity, and are there equivalent but alternative
    strategies to viviparity?
5. Is there one general hypothesis which best explains all cases
    of the evolution of viviparity?

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RESULTS

The Geographic Distribution of Viviparity

Sergeev (1940) presented a series of maps showing that in Eurasia the proportion of viviparous species was low in the south (e.g. 2% in the Crimea) and as high as 100% in the north. A somewhat similar pattern was documented for China. India, on the other hand, was shown to have a low proportion of viviparous reptiles. Sergeev also presented data on altitudinal changes in proportion of viviparous species in one area of Russia; the per cent of total reptile species which were viviparous increased to 100% at high elevations. We have prepared similar analyses of data for faunas not extensively considered by Sergeev, but which are now fairly well known, to determine whether the pattern suggested by him occurs worldwide. However, in addition, we include absolute numbers of species as well as proportions.

Table 2 shows total numbers of lizard and snake species occurring in various latitude zones in the United States. In the southernmost zone we included only those Mexican species which also occurred within the political boundaries of the United States. Among lizards, the proportion of viviparous species is essentially constant below 10% through latitude 45°N, and then increases dramatically to 22% between latitudes 45°N and 50°N. Proportional viviparity among snakes is higher than among lizards and is essentially constant through latitude 50°N. Above that latitude, the proportion of viviparous snakes increases markedly to 63% between latitude 50°N and 55°N and 100% above latitude 55°N. However, as Column 3 in Table 2 clearly demonstrates, there is a general decline in the total number of snake and lizard species as one proceeds north, until above latitude 50°N the total squamate fauna is represented by fewer than 10 species. In other words, the increasing proportion of viviparous

TABLE 2

COMPARISON OF NUMBERS OF OVIPAROUS AND VIVIPAROUS SPECIES
OF SNAKES AND LIZARDS FROM DIFFERENT LATITUDINAL ZONES IN
NORTH AMERICA[1]

Latitude–°N	Lizards			Snakes			All Squamates		
	O	V	%V	O	V	%V	O	V	%V
25-30	63	6	8.7	57	37	39.4	120	43	26.4
30-35	71	8	10.1	58	45	43.7	129	53	29.1
35-40	46	5	9.8	45	41	47.7	91	46	33.6
40-45	25	2	7.4	27	24	47.1	52	26	33.0
45-50	7	2	22.2	12	11	47.8	19	13	40.6
50-55	0	0	-	3	5	62.5	3	5	62.5
55-60	0	0	-	0	1	100	0	1	100
Total species considered	76	11		65	50		141	61	

[1]Species lists were taken from Logier and Toner (1961), Stebbins (1966), and
Conant (1975). The number of species in all categories at 25°–30°N is actually
higher than indicated by the figure since species from northern Mexico that do not
occur in the U.S. were not included. O = oviparous, V = viviparous.

species at high latitudes is due not to an increase in their number but
to a more rapid decline in the numbers of oviparous species.
Raymond Huey (pers. comm.) has shown us maps of North America
on which he used a quadrat method to plot proportions of viviparous
lizards and snakes in much greater detail than presented by us. His
figures differ slightly from ours but the overall trends are the same.

Because Sergeev and others have emphasized the role of temper-
ature in the evolution of viviparity and because latitude is not
perfectly correlated with temperature, we used isotherm maps
(Visher, 1954) overlaid onto geographic distributions of North Ameri-
can reptiles to determine changes in proportion of viviparous species
with changes in temperature regimes. We used summer isotherms
because of our assumption that these were most relevant to reproduc-
tive adaptations of reptiles, most of which produce eggs or litters
during the summer in temperate regions. The pattern of change in
proportion of viviparous species with isotherms (Table 3) is essentially
the same as that with latitude (Table 2). Consequently, for subse-
quent presentations we have relied on latitude as the independent
variable in discussing geographic trends in viviparity.

To focus closely on the fauna of much smaller, but well-studied,
geographic areas within the southern and northern U.S., we chose the
herpetofaunas of Alabama and of Michigan (Table 4). Our expecta-
tion from the broad geographic trends (Tables 2 and 3) was that the
proportion of viviparous species in the fauna of Michigan would be
considerably higher that that in Alabama (Mount, 1975). This
expectation is true for the squamate faunas which are comprised of

TABLE 3

COMPARISON OF NUMBERS OF OVIPAROUS AND VIVIPAROUS SPECIES OF SNAKES AND LIZARDS OCCURRING IN DIFFERENT THERMAL ZONES IN THE UNITED STATES[1]

Isotherm-°F	Lizards			Snakes			All Squamates		
	O	V	%V	O	V	%V	O	V	%V
80-85	63	5	7.4	60	37	38.1	123	42	25.5
75-80	51	3	5.6	47	35	42.7	98	38	27.9
70-75	45	4	8.2	41	32	43.8	86	36	29.5
65-70	25	4	14.0	23	22	48.9	48	26	35.1
60-65	8	4	33.3	11	14	56.0	19	18	48.6
Total Species Considered	76	11		65	50		141	61	

[1]Isotherm zones are based on average summer (June-August) temperatures over a 20+ year period (from Atlas of American Agriculture, 1936). Species ranges were ascertained from Stebbins (1966) and Conant (1975). O = oviparous. V = viviparous.

TABLE 4

COMPARISON OF NUMBERS OF OVIPAROUS AND VIVIPAROUS SPECIES OF SQUAMATE REPTILES FROM MICHIGAN (42°-45°N) AND ALABAMA (30°-35°N)[1]

	ALABAMA			MICHIGAN		
	O	V	%V	O	V	%V
Lizards	11	0	0	1	0	0
Snakes	20	20	50.0	7	10	58.9
Total Squamates	31	20	39.2	8	10	55.6

[1]Species lists were taken from Conant (1975) and Mount (1975). O = oviparous. V = viviparous.

39% viviparous species in Alabama and of 56% in Michigan. However, more significantly, the Michigan herpetofauna is impoverished and the absolute number of viviparous species in Alabama (20) is twice that found in Michigan; in both areas, all viviparous species are snakes.

If cold temperature is the predominant factor in its evolution, viviparity should be most frequent in those species whose distributions are restricted to northerly regions or high elevations. Of 15 such species in the U.S. herpetofauna (Table 5), 7 are egg-layers and 8 are live-bearers. The per cent viviparous (53%) is not significantly different ($\chi^2 = 3.34$; $P > .06$) from that among all squamates reaching these latitudes (33%; Table 2). Clearly, intraspecific comparisons of reproductive mode in different climatic regions would be more

TABLE 5

NORTH AMERICAN SQUAMATES OCCURRING MOSTLY ABOVE LATITUDE
40°N OR AT HIGH ELEVATIONS[1]

SNAKES

VIVIPAROUS	OVIPAROUS
Clonophis kirtlandi	Elaphe vulpina
Thamnophis butleri	Contia tenuis
Thamnophis radix	Opheodrys vernalis
Thamnophis ordinoides	Lampropeltis zonata
Thamnophis brachystoma	Lampropeltis pyromelana
Charina bottae	

LIZARDS

VIVIPAROUS	OVIPAROUS
Gerrhonotus coeruleus	Eumeces skiltonianus
Phrynosoma douglasi	Sceloporus graciosus

			% viviparous
Total	8	7	53.3
Total of all species at +40°N	26	52	33.3

[1]Range determinations from Conant 1975 and Stebbins 1966.

meaningful, but as discussed below the occurrence of both oviparity
and viviparity within a single species is extraordinarily rare. There-
fore, interspecific comparisons are used throughout this paper.

Australia has an exceedingly diverse squamate fauna distributed
over a wide geographical area not greatly confounded by numerous
montane regions or major topographic relief (Cogger, 1975). All of
the lizard families show the same latitudinal trends in numbers of
species (Table 6), but only the skinks contain viviparous representa-
tives. Species numbers are lowest in the tropical north and in the
temperate south and highest in the middle latitudes. The proportion
of viviparous skinks increases steadily southward from the tropics. On
Tasmania nearly 70% of the lizards are viviparous but there is also a
concomitant marked decline in total numbers of lizard species.
Australian snakes (Table 7), like the lizards, show a fairly steady
increase in per cent viviparous, from 26% in the tropical north to
twice that proportion in the temperate south, and to 100% in
Tasmania. As among North American reptiles, the snakes at all
latitudes show a much higher proportion of viviparity than lizards do.

On a finer geographic scale, we have selected various countries
with fairly well-studied faunas to compare the proportion of vivipa-

TABLE 6

COMPARISON OF NUMBERS OF OVIPAROUS AND VIVIPAROUS SPECIES OF LIZARDS FROM DIFFERENT LATITUDINAL ZONES IN AUSTRALIA[1]

LATITUDINAL ZONE-°S	Gekkonidae O	Pygopodidae O	Agamidae O	FAMILY Varanidae O	Scincidae O	V	%V	All Species O	V	%V
10-15	20	4	16	12	27	6	18.2	79	6	7.1
15-20	28	5	28	15	45	13	22.4	121	13	9.7
20-25	41	12	26	15	40	20	33.3	134	20	13.0
25-30	43	18	38	10	46	31	40.3	155	31	16.7
30-35	38	21	28	6	40	36	47.4	133	36	21.3
35-40	13	13	7	2	16	23	60.0	51	23	31.1
40-45(Tasmania)	0	0	1	0	3	8	72.7	4	8	66.7
Total Species Considered	62	28	53	21	132			296		

[1]Species lists and ranges were taken from Cogger (1975). Some data on reproductive mode were also taken from Littlejohn and Rawlinson (1971). O = oviparous. V = viviparous.

TABLE 7

COMPARISON OF NUMBERS OF OVIPAROUS AND VIVIPAROUS SPECIES OF SNAKES FROM DIFFERENT LATITUDINAL ZONES IN AUSTRALIA[1]

LATITUDINAL ZONE-°S	Typhlopidae (All O)	Boidae* (All O)	Acrochordidae (Both V)	FAMILY Colubridae**		Elapidae		All Species		
				O	V	O	V	O	V	%V
10-15	12	7	2	5	5	7	4	31	11	26.2
15-20	11	8	2	5	5	7	10	31	17	35.4
20-25	14	6	0	0	4	7	14	27	18	40.0
25-30	12	4	0	0	3	6	17	19	20	51.3
30-35	10	3	0	0	2	4	21	17	23	57.5
35-40	9	1	0	0	2	4	14	14	16	53.3
40-45(Tasmania)	0	0	0	0	0	0	3	0	3	100
Total Species Considered	22	9	2	5	5	9	26	45	33	

*Excludes Liasis albertisii from Torres Straits
**Excludes Stegonotus parvus from Torres Straits

[1]Species lists and ranges were taken from Cogger (1975). Reproductive type could not be ascertained for species in a dozen genera of elapids so these are not included in the comparison. Some data on reproductive mode were taken from Littlejohn and Rawlinson (1971). O = oviparous. V = viviparous.

rous and oviparous species in both tropical and additional temperate areas. The impoverished reptile fauna of temperate Chile (Donoso-Barros, 1966) contains a high proportion of viviparous species (Table 8). Lizards constitute almost all of the herpetofauna and the majority of these belong to the single genus *Liolaemus*, most of which occur at high elevations in the Andes. The reptile fauna of temperate Japan (Table 8) is likewise impoverished (19 species) but contains only 2 viviparous species (Fukada, 1965; Stejneger, 1907).

Tropical areas of the world are represented in our study by Borneo, Ecuador, Uganda, Costa Rica, Cambodia, and South Vietnam (Table 9). Lloyd, Inger and King (1968) recorded 76 Bornean squamates for which reproductive information was available. Of these, only 8 were viviparous. Among the snakes of Uganda (Pitman, 1974) breeding habits are known for 71 species of which 8 are viviparous. Taylor (1951, 1954, 1956) recorded 66 species of lizards and 128 species of snakes in Costa Rica; 12% of each group are viviparous. In one local area in Ecuador (Duellman, pers. comm.) 1 of 30 species of lizards (including amphisbaenians) is viviparous as are 10 of 53 snake species. Saint Girons and Pfeffer (1972) recorded 37 species of Cambodian snakes, of which 10 are viviparous, but this study apparently did not represent the entire snake fauna. In neighboring South Vietnam where a more complete list is available (Campden-Main, 1970) more than 21% of the 72 species for which reproductive habits are known are viviparous.

We also considered detailed comparisons by other investigators of the correlation of elevation with viviparity in several areas of the

TABLE 8

NUMBERS OF OVIPAROUS AND VIVIPAROUS SPECIES OF SNAKES AND LIZARDS FROM CHILE AND JAPAN[1]

CHILE (18°–55°S Lat.)	Oviparous	Viviparous	%Viviparous
Lizards	24*	29**	54.7
Snakes	4	1	20.0
Total Squamates	28	30	51.7

JAPAN (31°–45°N Lat.)	Oviparous	Viviparous	%Viviparous
Lizards	5	1	16.7
Snakes	12	1	7.7
All Squamates	17	2	10.5

*9 belong to the genus *Liolaemus*
**21 belong to the genus *Liolaemus*

[1]Data for Chile are from Donoso-Barros (1966), those for Japan from Stejneger (1907) and Fukada (1965). Sea snakes and species of unknown reproductive mode were omitted.

world. Test, Sexton, and Heatwole (1966) recorded reptile species at low elevation (below 425 meters) and higher elevation (1000–1500 meters) in Venezuela. Viviparous lizards did not occur in either locality, but 2 of 9 snake species at low elevations and 2 of 14 species at high elevations are live-bearers. In the 37 squamate species from these two habitats, fewer than 10% are viviparous—a figure comparable to most other tropical regions (Table 9) and to the Amazon Basin in Peru where Dixon and Soini (1975) recorded one viviparous lizard species among a total of 31.

In East Africa, Greer (1968a) compared species of snakes and lizards in three altitudinally distributed habitat zones. About 11% of the 93 coastal plain (10–1000 feet) squamate species for which

TABLE 9

NUMBERS OF OVIPAROUS AND VIVIPAROUS SPECIES OF SQUAMATES FROM TROPICAL AREAS[1]

	Oviparous	Viviparous	%Viviparous
BORNEO (4°N–4°S Lat.)			
Lizards	29	5	14.7
Snakes	39	3	7.1
Total Squamates	68	8	10.5
UGANDA (4°N–1°S Lat.)			
Snakes	63	8	11.3
COSTA RICA (8°–12°N Lat.)			
Lizards	58	8	12.1
Snakes	113	15	11.7
Total Squamates	171	23	11.9
ECUADOR (0° Lat.) (Santa Cecilia)			
Lizards	29	1	3.3
Snakes	43	10	18.9
Total Squamates	72	11	13.3
CAMBODIA (11°–14°N Lat.)			
Snakes	27	10	27.1
SOUTH VIETNAM (8°–18°N Lat.)			
Snakes	58	16	21.6
Total Tropical Lizards	116	14	10.7
Total Tropical Snakes	343	62	15.3
Total Tropical Squamates	459	76	14.2

[1]The following countries are represented: Borneo (Lloyd, Inger and King, 1968), Uganda (Pitman, 1974), Costa Rica (Taylor 1951, 1954, 1956), Ecuador (Duellman, pers. comm.), Cambodia (St. Girons and Pfeffer, 1972), and South Vietnam (Campden-Main, 1970). Omissions as in Table 8. Also, the Cambodian list for snakes is believed to be incomplete. Grand totals may be slightly high due to duplications of species between areas in some instances.

reproductive mode was known are viviparous as are about 10% of the 119 species of upland savannas (1000–6000 feet). Eleven of 14 species in the impoverished montane fauna (5000–12000 feet elevation) are viviparous. The only species that was classed by Greer as a high elevation endemic (the lizard *Algyroides alleni*) was oviparous.

Greene (1970), using data from Martin (1958), showed that the proportion of viviparous squamates increases fairly steadily with elevation from sea level to over 2000 meters in the Gomez Farias region of Mexico. At the highest elevation 100% of the species are viviparous (compared to as few as 10% at some low elevations). The reptile fauna diminished rapidly at high elevations with only five species occurring above 2000 meters (Table 10); however, among lizards, a general trend is apparent of increasing numbers of viviparous species with altitude, as well as an increasing proportion.

In the sample of the world's tropical species considered by us, about 14% are viviparous. In contrast, primarily temperate faunas display higher percentages of viviparity with roughly one-third of the species viviparous at middle latitudes, and a majority at high latitudes. One difference between lizards and snakes is that the proportion of viviparines among the latter is higher in temperate areas than in the tropics. Although amphibians are not considered in this paper, we are aware that the primarily tropical caecilians show a high (50%) proportional viviparity (M. H. Wake, pers. comm.). A detailed comparison of distribution of oviparous and viviparous species of these amphibians could be instructive.

TABLE 10

NUMBERS OF OVIPAROUS AND VIVIPAROUS SPECIES OF SNAKES AND LIZARDS AT DIFFERENT ELEVATIONS IN THE GOMEZ FARIAS REGION OF MEXICO[1]

NUMBER OF SPECIES	ELEVATION (m)								
	0-250	250-500	500-750	750-1000	1000-1250	1250-1500	1500-1750	1750-2000	2000-2250
Lizards — O	11	11	11	8	5	3	3	0	0
V	1	2	2	4	5	7	7	6	4
Snakes—O	18	19	14	13	14	7	7	2	0
V	6	1	2	2	4	5	5	4	1
All Squamates—O	29	30	25	21	19	10	10	2	0
V	7	3	4	6	9	12	12	10	5
% Viviparous									
Lizards	8.3	15.4	15.4	33.3	50.0	70.0	70.0	100	100
Snakes	25.0	5.0	12.5	13.3	22.2	41.7	41.7	66.7	100
All Squamates	19.4	9.1	13.8	22.2	32.1	54.5	54.5	83.3	100

[1]Data were taken from Greene (1970). O = oviparous. V = viviparous.

We have not compared the geographic distribution of oviparous and viviparous species within closely related taxa showing both reproductive modes, although such an exercise might be highly illuminating. We hope, however, that investigators with detailed knowledge of appropriate groups will be stimulated to undertake such comparative studies in the future.

The Taxonomic Distribution of Viviparity

Viviparity is widespread in squamates and presumably evolved independently in many families, about half of which are indicated in Table 11.

In addition to families containing genera that have both oviparous and viviparous species (and therefore shown in Table 11), the following families have some or all viviparous species: lizards—

TABLE 11

GENERA OF SNAKES AND LIZARDS WHICH ARE KNOWN TO HAVE BOTH OVIPAROUS AND VIVIPAROUS SPECIES[1]

LIZARDS

Agamidae
  Phrynocephalus   Smith 1935; Rustamov and Shammakov
                                       1967

Anguidae
  Diploglossus   Greer 1967a
  Gerrhonotus
  (including *Barisia*)   Fitch 1970

Chamaeleontidae
  Chamaeleo   Smith 1935, Bustard 1965a, Fitch 1970

Lacertidae
  Lacerta   Smith 1951

Iguanidae
  Corytophanes   Alvarez del Toro 1960; McCoy 1968
  Liolaemus   Donoso—Barros 1966
  Phrynosoma   Stebbins 1954
  Sceloporus   Stebbins 1954

Scincidae
  Eumeces   Axtell 1960; Fitch 1954
  Leiolopisma   Barwick 1959; Worrell 1964
  Leptosiaphos   Loveridge 1936, 1942; Fitch 1970
  Mabuya   Smith 1935
  Riopa (=Mochlus)   FitzSimons 1962; Sprawls 1973;
                                       Pienaar 1966
  Scincella   Smith 1935
  Sphenomorphus   Greer and Parker 1967; Cogger 1975
  Tribolonotus   Greer and Parker 1968
  Lerista   Greer 1967b

TABLE 11 (continued)

SNAKES

Typhlopidae	
Typhlops	Wall 1918; Smith 1943
Colubridae*	
Elaphe	Pope 1935
Aparallactus	FitzSimons 1962; Sprawls 1973; Pitman 1974
Natrix	Fitch 1970
Helicops	Fitch 1970; Rossman 1973
Coronella	Street, 1973
Elapidae	
Cacophis	Worrell 1964; Kinghorn 1964; Cogger 1975
*Calliophis (=Callophis)***	Neill 1964; Fukada 1965
Viperidae	
Echis	Wall 1918; Smith 1943; Duff-MacKay 1965; Mendelssohn 1965; Pitman 1974
Vipera	Mendelssohn 1963; Fitch 1970
Aspis	Mendelssohn 1963
Crotalidae	
Agkistrodon	Pope 1935
Trimeresurus	Pope 1935

Meizodon was stated by Neill (1964) to be viviparous but we were unable to find supporting data for either reproductive type.
**Neill (1964) stated that a *"Callophis"* species was probably viviparous, although we have found no evidence of documentation of viviparity. Another species is definitely oviparous (Fukada 1965).

[1]The references indicated for each genus collectively support the conclusion that both types of reproduction occur.

Amphisbaenidae, Anniellidae, Cordylidae, Gekkonidae, Xantusiidae, Xenosauridae; snakes—Acrochordidae, Boidae, Hydrophiidae, Uropeltidae. This is markedly different from the situation in crocodilians and turtles, all of which are oviparous. The contrast can be placed in clear perspective among North American reptiles by noting that turtles comprise 20% of the reptile species between latitudes 40 and 45 and, yet, show no instances in which viviparity, or even egg-retention, is characteristic for a species. Over two dozen squamate genera contain both oviparous and viviparous species (Table 11), demonstrating that closely related species may differ in reproductive mode, and thereby emphasizing the extent of independent origin of viviparity. It is not widely appreciated that several species also have been reported to be both oviparous and viviparous (Table 12), but we think that only one

TABLE 12
SPECIES OF SNAKES AND LIZARDS IN WHICH BOTH OVIPARITY AND VIVIPARITY HAVE BEEN REPORTED

SPECIES	SOURCE
Lacerta vivipara	Lantz 1927; Weekes 1934; Panigel 1956; Fukada 1965
Mabuya quinquetaeniata	FitzSimons 1943, Loveridge 1953, Schmidt & Inger 1957; Fitch 1970
Sceloporus variabilis	Werler 1951; Brattstrom and Howell 1954; Alvarez del Toro 1960
Sceloporus aeneus	Davis & Smith 1953; Thomas and Dixon, 1976
Typhlops diardi	Wall 1918; Smith 1943
Boa constrictor	Hoover 1936
Python regius	Pope 1961
Diadophis punctatus	Ditmars 1936; Peterson 1956
Xenodermus javanicus	Kopstein 1938; Smith 1943; Taylor 1965
Cacophis kreffti	Worrell 1964; Kinghorn 1964; Cogger 1975
Echis carinatus	Wall 1918; Smith 1943; Mendelssohn 1965; Pitman 1974
Trimeresurus okinavensis	Fukada 1964, 1965

of the examples (*Sceloporus aeneus*) in Table 12 can be cited with any assurance as demonstrating both conditions. However, this phenomenon of reproductive bimodality within a single species could be of vital importance in understanding the evolution of viviparity, so each reported case deserves detailed discussion.

Some reported examples of reproductive bimodality may result from taxonomic confusion of species. *Typhlops diardi* was recorded by Wall (1918) as "attaining a considerable development inside the egg before the latter is discharged." This suggests that the species is an egg-layer, although Wall did not actually record egg deposition. Possibly, the specimens observed by him were, in fact, viviparous as reported by Smith (1943) or the two authors may have been reporting on different species as suggested by Fitch (1970). *Mabuya quinquetaeniata* is cited as oviparous by Loveridge (1936; 1953) and by Schmidt and Inger (1957), but as viviparous by FitzSimons (1943). Fitch (1970) suggests that viviparity occurs in this species in the cooler southern part of its range. However, two species could be involved. The report of viviparity in *Sceloporus variabilis* based on

dissection by Werler (1951) is somewhat surprising in view of the documentation of egg-laying habits in this species (Brattstrom and Howell, 1954; Alvarez del Toro, 1960; Fitch, 1970). Werler dissected a zoo-kept female that contained "7 developing embryos, partially enclosed in yolk sacs." Werler may have observed oviductal embryos in a normally egg-laying species prior to shell formation. It also seems possible that a very similar viviparous species was confused with *S. variabilis*.

Some reports of viviparity in normally egg-laying species, or vice versa, may represent instances in which the investigator did not understand the biological implications of his observations. For example, a single report of egg-laying by the boa constrictor (*Boa constrictor*) was published by Hoover (1936) and cited by Fitch (1970) as a case of a "normally viviparous ... [species that] ... occasionally at least can still produce shelled eggs." In this instance the captive boa produced two normal young as well as eggs with "leathery shelled membranes" which enclosed young of approximately the same size and appearance as the two normal ones. We suggest that the author misinterpreted dried membranes which normally enclose young snakes at birth as "shells." A similar misinterpretation may have occurred in the case of the pit viper *Trimeresurus okinavensis* (Fukada, 1964). In his lab, this normally live-bearing species laid eggs covered with a thick, shell-like membrane. The eggs "hatched" within 1–4 days of laying. Fukada (1965) later emphasized that the eggs were laid in highly unnatural lab situations and that the embryos were surrounded by heavy membranes rather than shells. *Cacophis kreffti* was reported by Kinghorn (1964) to produce six to ten young. Worrell (1964) recorded "two or three large eggs." However, Worrell could have been referring to large membrane-enclosed eggs which are characteristic of all viviparous species. We feel that Cogger (1974) implies such an interpretation for a related species (*C. squamulosus*) because of his statement that they produce young in "unshelled egg-sacs" which hatch shortly after laying.

We find difficulty in offering explanations for some reports of reproductive bimodality. For example, the normally egg-laying ringneck snake (*Diadophis punctatus*) has twice been reported viviparous (Ditmars, 1936; Peterson, 1956). Both reports are of baby snakes found in cages containing only adult female ringneck snakes. Several careful, detailed studies of the biology of the species (Blanchard, 1930, 1937; Myers, 1965; Fitch 1975) offer no evidence for viviparity or unduly long oviductal egg-retention. A somewhat similar, though undocumented, case of live-bearing in a normally egg-laying species was reported for *Python regius* (Pope, 1961). This report, the only one known to us of any instance of live-bearing in any member of the genus *Python,* is accompanied only by the statement that this species has been "credited with laying as well as with giving birth." Likewise, Taylor (1965) stated that the snake *Xenodermus javanicus*

is "ovoviviparous." Taylor does not reveal the evidence for this statement nor even mention the discrepancy between his observation and that of others. Kopstein (1938), in particular, made a careful study of the egg-laying habits of this species, and Smith (1943) reported it as laying 2–4 eggs. Duff-Mackay (1965) reported oviparity in the normally viviparous *Echis carinatus* (Wall, 1921; Smith, 1943). Duff-Mackay discovered three sets of eggs laid by some individuals among 3000 *E. carinatus* maintained in captivity over the course of a study in Kenya. It appears possible that these eggs were laid by some oviparous snakes of another species inadvertently mixed in the enormous sample. In any event none of the eggs hatched, so that certain identification was not possible. Pitman (1974) cited no examples, other than Duff-Mackay's, of oviparity in this African snake. However, Mendelssohn (1965) cited additional reports of oviparity in African populations and viviparity in Asian populations of this wide-ranging species.

One example of reproductive bimodality within a single species (*Lacerta vivipara*) has been so pervasive and so widely accepted in the literature that detailed consideration is essential. Lantz (1927) reported finding 60 eggs beneath a stone in the Pyrenees Mountains. Some of these "hatched" immediately as might be expected of a viviparous species such as *L. vivipara*. Others were shelled and contained embryos in varying stages of development. From this observation Lantz concluded that this species in that region had retained its presumed ancestral oviparous condition. Despite the absence of further documentation of oviparity, *L. vivipara* is now generally acknowledged to be reproductively bimodal. This is clear from several reports in the literature: "The European Lizard, *Lacerta vivipara*, which bears living young throughout most of its range, lays eggs in the Pyrenees" (Goin and Goin, 1971; p. 113). "The Common Lizard (*Lacerta vivipara*), a species that bears living young, as its scientific name indicates, is an egg-layer in the Iberian Peninsula, i.e. in the south. In the farthest north, however, the summer is evidently too short for the development and birth of the young . . . " (Mertens, 1960; p. 76). "In the Pyrenees Mountains the species retains oviparous habits, and eggs with parchment-like shells are laid" (Fitch, 1970, p. 106). Interestingly, some of the examples of live-bearing *L. vivipara* used by Weekes (1934) in her study of corpora lutea came from the Pyrenees. To our knowledge, in the half-century since publication of Lantz's observation only two authors have questioned his interpretation. Panigel (1956) dismissed this as a case of premature egg-laying, as did Packard, Tracy, and Roth (1977). We, too, think the interpretation by Lantz is questionable. The fact that 60 eggs were found beneath a single stone indicates, as Lantz was aware, that several individuals deposited eggs in this same location. It seems possible, if not likely, that the eggs found by Lantz were those of more than one species, at least one of which was *L. vivipara,* repre-

sented by the "eggs" that hatched immediately, and one a sympatric egg-laying species such as *Lacerta muralis* or *L. agilis*. Such interspecific communal nesting among reptiles has been previously reported (Brodie, Nussbaum, and Storm, 1969). In any event, verification of oviparity in this species through additional field research is required.

One report of intraspecific reproductive bimodality seems to be well-documented. The lizard *Sceloporus aeneus* has been reported oviparous in some areas of the range and viviparous in others (Davis and Smith, 1953). However, these authors suggested that the viviparous form (subspecies *S. a. bicanthalis*) deserves specific status on the basis of its geographic distribution and absence of intergradation with *S. a. aeneus*. The taxonomic status of *S. a. bicanthalis* was not changed by Smith and Smith (1976). Thomas and Dixon (1976) in a careful re-evaluation of the races of *S. aeneus* report that no characters other than reproductive mode consistently separate these two subspecies. Therefore, it appears that oviparity and viviparity occur within the same subspecies of *S. aeneus,* and that both modes occur at high elevations. We hope this discussion will stimulate others to seek documentation of further instances of reproductive bimodality, some of which may have been obscured because reproductive mode itself formed the basis for the taxonomic separation of species.

Incubation and Gestation Times

Because Sergeev (1940) implicated long incubation periods in cold environments as a selective pressure favoring viviparity, we have sought evidence that high latitude or high elevation species generally have long incubation periods compared with those in warmer areas. We also examine the related question of whether live-bearing species have generally shorter periods of development than egg-laying species, particularly in the same geographic location. If cold environments do prolong developmental periods then these may be longer in oviparous species than in sympatric viviparous ones which can better control the temperature of developing embryos through behavioral thermoregulation.

Tables 13 and 14 include a large sample of incubation and gestation periods for tropical and temperate reptiles. These data have been plotted as frequency histograms (Fig. 1) to provide a graphic view of comparative incubation and gestation periods. Data for lizards and snakes were plotted separately initially, but in the absence of any obvious differences in any category were combined in Figure 1. Because egg-guarding, as will be brought out later, has been viewed as an alternative to viviparity, species practicing egg-guarding are also indicated.

There is no evidence for more rapid development times in either tropical oviparous or viviparous species when compared to temperate ones. However, the variance in development times appears to be

TABLE 13

VARIATION IN INCUBATION PERIODS AMONG AND WITHIN SQUAMATE SPECIES[1]

	SPECIES	FAMILY	INCUBATION PERIOD (Days)	REFERENCE
1.	*Saiphos equalis*	Scincidae	7-14	Cogger 1975
2.	*Eumeces callicephalus***	Scincidae (TR)	9 (lab at 87°F)	Zweifel 1962
	*Eumeces callicephalus***	Scincidae (TR)	19-23	Campbell and Simmons 1961
3.	*Opheodrys vernalis*	Colubridae	14 (approx.)	Blanchard 1933
	Opheodrys vernalis	Colubridae	30 (approx.)	Stille 1954
4.	*Helicops angulatus*	Colubridae	16-17	Rossman 1973
5.	*Natrix stolata***	Colubridae (TR)	19	Minton 1966 (from Fitch 1970)
	*Natrix stolata***	Colubridae (TR)	30	Wall 1921; Pope 1935
6.	*Elaphe dione*	Colubridae	21	Langhammer (Pers. Comm.)
	Elaphe dione	Colubridae	29	Pope 1935
7.	*Takydromus tachydromoides*	Lacertidae	26-54	Fukada 1965
	Takydromus tachydromoides	Lacertidae	32-38 (25-28°C; lab)	Telford 1969
8.	*Scincella laterale*	Scincidae	28 (estimated)	Johnson 1953
	Scincella laterale	Scincidae	29-33	Lewis 1951
9.	*Natrix tigrina*	Colubridae	29-45	Fukada 1965
10.	*Draco volans*	Agamidae (TR)	29	Kopstein 1938
	Draco volans	Agamidae (TR)	30-42	Alcala 1967
11.	*Sceloporus undulatus*	Iguanidae	29-76 (lab 25-35°C)	Sexton and Marion 1974
	Sceloporus undulatus	Iguanidae	33-50	Carpenter 1960
	Sceloporus undulatus	Iguanidae	49-58	Crenshaw 1955
12.	*Anolis carolinensis*	Iguanidae	30	Gordon 1956
13.	*Anolis limifrons*	Iguanidae (TR)	30(field)	Sexton, Heatwole, Meseth 1963

14.	*Hemidactylus flaviviridis*	Gekkonidae	30 (estimated)	Mahendra 1936
15.	*Phrynocephalus helioscopus*	Agamidae	30-40 (estimated)	Rustamov and Shammakov 1967
16.	*Typhlops schlegeli*	Typhlopidae	30-42	FitzSimons 1962
16a.	*Pseudocerastes fieldi*	Viperidae	30-31	Mendelssohn 1965
17.	*Eumeces egregius***	Scincidae	31-51	Mount 1963
18.	*Natrix vibakari*	Colubridae	34-37	Fukada 1965
19.	*Psammophylax rhombeatus***	Colubridae	35-42	FitzSimons 1962
20.	*Crotaphytus wislizeni*	Iguanidae	35-49	McCoy 1967
	Crotaphytus wislizeni	Iguanidae	59 (field estimate)	Montanucci 1965
	Crotaphytus wislizeni	Iguanidae	79-84	Montanucci 1967
21.	*Opheodrys aestivus*	Colubridae	35-88	Fitch 1970
22.	*Tretanorhinus variabilis*	Colubridae (TR)	35	Petzold 1967
23.	*Lampropeltis triangulum*	Colubridae	36-50	Fitch 1970
24.	*Hemidactylus turcicus*	Gekkonidae	37-45	Rose and Barber 1968
25.	*Typhlops braminus*	Typhlopidae (TR)	38	Fitch 1970
26.	*Vipera xanthina*	Viperidae	39-62	Fitch 1970
27.	*Hemiphyllodactylus typus*	Gekkonidae (TR)	40 +	Kopstein 1938
28.	*Eumeces septentrionalis***	Scincidae	40-52	Breckenridge 1943
29.	*Elaphe quadrivirgata***	Colubridae	40-57	Fukada 1965
30.	*Trimeresurus flavoviridis*	Crotalidae	40-41	Fukada 1965
31.	*Natrix vittata*	Colubridae	40-60	Kopstein 1938
32.	*Calotes versicolor*	Agamidae	42-45(field)	Asana 1931
	Calotes versicolor	Agamidae	42	Pandha and Thapliyal 1967

[1]Records are listed in order of increasing number of days, with parenthetical qualifiers where appropriate. Unless indicated, eggs were known or assumed to have been hatched at unreported "room temperatures." When a species is represented by more than one reference, the shortest recorded incubation period is used to determine its position in the list. For consistency, the "weeks" and "months" used in some references are converted to 7 and 30 days. Egg-guarding species for which incubation time is unknown are listed at end.
** = Egg Guarding Species. (TR) = Tropical Species.

TABLE 13 (continued)

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	SPECIES	FAMILY	INCUBATION PERIOD (Days)	REFERENCE
33.	*Coleonyx variegatus*	Gekkonidae	42 (estimated)	Parker 1972
34.	*Eumeces fasciatus***	Scincidae	42 (approx.)	Fitch 1954
35.	*Agkistrodon rhodostoma***	Crotalidae (TR)	42-47	Smith 1943
36.	*Coluber constrictor*	Colubridae	43-63	Fitch 1963a
37.	*Masticophis flagellum*	Colubridae	44	Fitch 1970
38.	*Lampropeltis calligaster*	Colubridae	45-73	Fitch 1970
39.	*Dinodon orientale*	Colubridae	45	Fukada 1965
40.	*Cnemidophorus inornatus*	Teiidae	46 (estimated)	Medica 1967
41.	*Cnemidophorus sexlineatus*	Teiidae	46-63 (lab and outdoor incubators)	Carpenter 1960
	Cnemidophorus sexlineatus	Teiidae	48-51 (field estimated)	Hardy 1962
42.	*Lacerta muralis*	Lacertidae	46 (80°F.)	Cooper 1965
	Lacerta muralis	Lacertidae	160 (65-70°F day; 55°F night)	Cooper 1965
43.	*Takydromus sexlineatus*	Lacertidae (TR)	47-62	Kopstein 1938
44.	*Heteronotia binoei*	Gekkonidae	47-48 (lab; 25°C)	Bustard 1969b
45.	*Elaphe conspicillata*	Colubridae	47-55	Fukada 1965
46.	*Carphophis vermis*	Colubridae	48-63	Clark 1970
47.	*Phrynosoma solare*	Iguanidae	48-51	Van Devender and Howard 1973
48.	*Gerrhonotus multicarinatus*	Anguidae	49	Burrage 1965
	Gerrhonotus multicarinatus	Anguidae	77 (estimated)	Goldberg 1972
49.	*Lacerta agilis*	Lacertidae	49-84 (field)	Smith 1951
50.	*Oedura tryoni*	Gekkonidae	49-51	Bustard 1967
51.	*Sceloporus scalaris*	Iguanidae	40 (estimated in field)	Newlin 1976
	Sceloporus scalaris	Iguanidae	49 (captivity)	Anderson 1962
52.	*Heterodon nasicus*	Colubridae	50-60	Platt 1969

53.	*Cnemidophorus hyperythrus*	Teiidae	50-55 (estimate)	Bostic 1966
54.	*Holbrookia texana*	Iguanidae	50 (captivity)	Cagle 1950
55.	*Eumeces obsoletus***	Scincidae	51	Fitch 1955
56.	*Cnemidophorus uniparens*	Teiidae	51-55	Maslin 1971
57.	*Natrix chrysarga*	Colubridae (TR)	51-61	Kopstein 1938
58.	*Elaphe climacophora***	Colubridae	51-64	Fukada 1965
59.	*Sonora episcopa*	Colubridae	53-67	Kassing 1961
60.	*Amblycephalus carinatus*	Colubridae (TR)	53-71	Kopstein 1938
61.	*Hypsiglena torquata*	Colubridae	53	Fitch 1970
62.	*Cnemidophorus neomexicanus*	Teiidae	54 (field estimate)	Medica 1967
	Cnemidophorus neomexicanus	Teiidae	59 (field estimate)	Christiansen 1971
	Cnemidophorus neomexicanus	Teiidae	57	Maslin 1971
63.	*Natrix subminiata*	Colubridae (TR)	54-70	Kopstein 1938
64.	*Gekko japonicus*	Gekkonidae	54	Fukada 1965
65.	*Python reticulatus***	Boidae	55-80	Fitch 1970
66.	*Farancia abacura***	Colubridae	55	Meade 1937
67.	*Lygosoma temminckii*	Scincidae (TR)	56	Kopstein 1938
68.	*Sonora semiannulata*	Colubridae	56	Fitch 1970
69.	*Leptodeira maculata*	Colubridae	57	Fitch 1970
70.	*Python molurus***	Boidae	57-66 (captivity)	Fitch 1970
71.	*Diadophis punctatus*	Colubridae	56-84	Blanchard 1930
	Diadophis punctatus	Colubridae	60 (average)	Fitch 1975
72.	*Elaphe guttata*	Colubridae	57-97	Fitch 1970
73.	*Oedura lesueuri*	Gekkonidae	58	Bustard 1967
74.	*Natrix triangulifera*	Colubridae (TR)	59-60	Kopstein 1938
75.	*Lampropeltis getulus*	Colubridae	59-81	Fitch 1970
76.	*Elaphe obsoleta*	Colubridae	60 (approx.)	Fitch 1963b
77.	*Sceloporus olivaceus*	Iguanidae	60	Blair 1960
78.	*Heterodon platyrhinos*	Colubridae	60 (approx.)	Platt 1969
79.	*Emoia atrocostata*	Scincidae (TR)	60	Alcala and Brown 1967
80.	*Agama agama*	Agamidae	60 (approx.)	Harris 1964
81.	*Oedura castelnauxi*	Gekkonidae	60	Bustard 1967
82.	*Crotaphytus collaris*	Iguanidae	60 (approx.)	Fitch 1956
83.	*Ptychodactylus hasseliquistii*	Gekkonidae	60-90 (approx.)	Werner 1965

TABLE 13 (continued)

	SPECIES	FAMILY	INCUBATION PERIOD (Days)	REFERENCE
84.	Sceloporus graciosus	Iguanidae	60 (estimate)	Tinkle 1973
	Sceloporus graciosus	Iguanidae	62	Woodbury and Woodbury 1945
85.	Philothamnus irregularis	Colubridae	60 (approx.)	Fitch 1970
86.	Natrix natrix	Colubridae	60 (approx.)	Fitch 1970
87.	Gehyra variegata	Gekkonidae	61-79 (lab at 25°C)	Bustard 1970a
88.	Xenodermus javanicus	Colubridae (TR)	61-65	Kopstein 1938
89.	Cnemidophorus exsanguis	Teiidae	62 (estimate)	Medica 1967
90.	Natrix piscator	Colubridae (TR)	62-89	Kopstein 1938
	Natrix piscator	Colubridae (TR)	87	Pope 1935
91.	Aplopeltura boa	Colubridae (TR)	63-69	Kopstein 1938
92.	Lampropeltis zonata	Colubridae	63	Fitch 1970
93.	Holbrookia maculata	Iguanidae	63-68 (estimate)	Walker and Tinkle (Unpl.)
94.	Rhinocheilus lecontei	Colubridae	64-79	Fitch 1970
95.	Pituophis melanoleucus	Colubridae	64-71	Fitch 1970
96.	Calamaria innaei	Colubridae (TR)	64-84	Kopstein 1938
97.	Boiga multimaculata	Colubridae (TR)	65-67	Kopstein 1938
98.	Arizona elegans	Colubridae	68	Fitch 1970
99.	Cnemidophorus tigris	Teiidae	68 (estimate)	Hoddenbach 1965
100.	Draco fimbriatus	Agamidae (TR)	68	Kopstein 1938
101.	Naja naja**	Elapidae (TR)	69-84	Smith 1943
	Naja naja**	Elapidae (TR)	88	Kopstein 1938
102.	Amphibolorus maculosus	Agamidae	70	Mitchell 1973
103	Calotes tympanistriga	Agamidae (TR)	70	Kopstein 1938
104.	Uta stansburiana	Iguanidae	70 (field estimate)	Tinkle 1967
	Uta stansburiana	Iguanidae	90 (field estimate)	Tinkle 1967
105.	Ophiophagus hannah**	Elapidae (TR)	70-77	Fitch 1970
106.	Oxyuranus scutellatus	Elapidae (TR)	70-98	Worrell 1964
107.	Cnemidophorus tesselatus	Teiidae	74-76 (field estimate)	Maslin 1971

108.	Dipsosaurus dorsalis	Iguanidae	75 (estimate)	Mayhew 1971
109.	Gehyra australis	Gekkonidae	75-101 (lab at 25°C)	Bustard 1969a
	Gehyra australis	Gekkonidae	139-148 (lab at 25°C)	Bustard 1969a
110.	Laticauda colubrina	Hydrophiidae	75 (TR)	St. Girons 1964
	& L. laticauda	Hydrophiidae		
111.	Gonatodes vittatus	Gekkonidae (TR)	75-94	Quesnel 1957
112.	Ophisaurus attenuatus**	Anguidae	75 (approx.)	Fitch 1967
113.	Naja melanoleuca	Elapidae (TR)	78	Fitch 1970
114.	Trimorphodon vandenbergi	Colubridae	79	Fitch 1970
115.	Leptodeira septentrionalis	Colubridae	79	Fitch 1970
116.	Lycodon subcinctus	Colubridae (TR)	79-83	Kopstein 1938
117.	Amphibolorus inermis	Agamidae	84-105 (estimate)	Pianka 1971
118.	Tantilla gracilis	Colubridae	83-84	Fitch 1970
119.	Maticora intestinalis	Elapidae (TR)	84	Kopstein 1938
120.	Calotes jubatus	Agamidae (TR)	84 +	Kopstein 1938
121.	Dendrophis boiga	Colubridae	85-86	Pope 1935
122.	Phyllodactlyus marmoratus	Gekkonidae	85-92 (lab at 25°C)	Bustard 1965b
	Phyllodactylus marmoratus	Gekkonidae	207	Waite 1929
123.	Dendrophis pictus	Colubridae (TR)	85-126	Kopstein 1938
124.	Boiga dendrophila	Colubridae (TR)	86	Kopstein 1938
125.	Oedura marmorata	Gekkonidae	88	Bustard 1967
126.	Ptyas mucosus**	Colubridae (TR)	89-95	Kopstein 1938
127.	Alsophis angulifer	Colubridae (TR)	89-95	Fitch 1970
128.	Causus defilippii	Viperidae	90-105	FitzSimons 1962
129.	Moloch horridus	Scincidae	90-132	Sporn 1965
130.	Dendrelaphis punctulatus	Colubridae (TR)	90 (approx.)	Worrell 1964
131.	Drymarchon corais	Colubridae	90-103	Fitch 1970
132.	Salvadora grahamiae	Colubridae	90-125	Fitch 1970
133.	Crotaphopeltis hotamboeia	Colubridae	90 (approx.)	Fitch 1970
134.	Oxyrhopus petolus	Colubridae (TR)	92-94	Test, Sexton and Heatwole 1966
135.	Gymnodactylus marmoratus	Gekkonidae (TR)	93 +	Kopstein 1938
136.	Masticophis lateralis	Colubridae	94	Fitch 1970
137.	Ptyas korros	Colubridae (TR)	98-101	Kopstein 1938
138.	Python sebae**	Boidae (TR)	100 (77-93° F)	Fitch 1970

TABLE 13 (continued)

	SPECIES	FAMILY	INCUBATION PERIOD (Days)	REFERENCE
139.	*Boiga jaspidea*	Colubridae (TR)	101 +	Kopstein 1938
140.	*Gonocephalus chamaeleontinus*	Agamidae (TR)	106-119	Kopstein 1938
141.	*Elaphe flavolineata*	Colubridae (TR)	107-109	Kopstein 1938
142.	*Amblyrhynchus cristatus*	Iguanidae (TR)	112 (lab)	Shaw 1966
143.	*Boiga drapiezi*	Colubridae (TR)	114 +	Kopstein 1938
144.	*Dendrophis formosus*	Colubridae (TR)	117 117	Kopstein 1938
145.	*Agama cyanogaster*	Agamidae (TR)	120 (estimate)	Robertson et al 1965
146.	*Dispholidus typus*	Colubridae	120-210 (approx.)	Fitch 1970
147.	*Ptychozoon kuhti*	Gekkonidae (TR)	122	Kopstein 1938
148.	*Kentropyx striatus*	Teiidae (TR)	124	Dixon, Staton, and Hendricks 1975
149.	*Boiga nigriceps*	Colubridae (TR)	136	Kopstein 1938
150.	*Psammophis sibilans*	Colubridae (TR)	143	Fitch 1970
151.	*Laticauda semifasciata*	Hydrophiidae	160 (lab at 28°C)	Fukada 1965
152.	*Varanus exanthamaticus*	Varanidae (TR)	170-175 (lab at 80-90°F)	Shaw 1963
153.	*Chamaeleo basiliscus*	Chamaeleontidae (TR)	173 (lab at 80-95°F)	Shaw 1960
154.	*Pholidobolus montium*	Teiidae	216	Bustard 1964
155.	*Chamaeleo chamaeleon*	Chamaeleontidae	220-262	Bons and Bons 1960
156.	*Leimadophis bimaculatus*	Colubridae (TR)	330 (approx.)	Fitch 1970

Addendum to Table 13.

The species below are egg-guarders but incubation times are not available:

|			
Most oviparous *Eumeces*	Fitch 1970	*Lachesis muta*	Mole 1924
Bungarus fasciatus	Pope 1935	*Leptotyphlops dulcis*	Hibbard 1964
Diploglossus bilobatus	Taylor 1956	*Neoseps reynoldsi*	Telford 1959
Diploglossus delasagra	Barbour and Ramsden 1919	*Ophisaurus* (all species)	Fitch 1970
Gerrhonotus liocephalus	Greene and Dial 1966	*Trimeresurus monticola*	Pope 1935
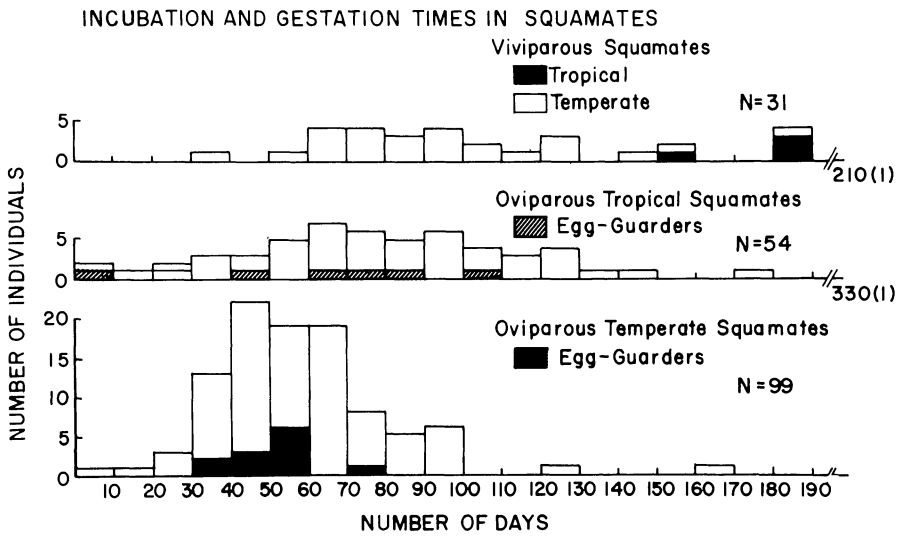
Fig. 1. Incubation and gestation times of oviparous and viviparous lizards and snakes. Abscissa shows number of days of incubation or gestation recorded in the literature (see text for explanation). Numbers of species are shown on the ordinate.

considerably greater in oviparous tropical species than in temperate ones. Because incubation times are nearly always reported as time to hatching *after* egg deposition, these times are not strictly comparable with gestation periods which are from ovulation to birth. Gestation times reported in Table 14 and Figure 1 are often based on the time from observed copulation to birth, possibly resulting in estimates longer than the actual gestation period. Greater comparability be-tween gestation and incubation periods would be. possible if the time from ovulation to egg deposition were known for oviparous species, but only a few data are available in the literature. Clark (1970) reported this period to be about 37 days for the worm snake (*Carphophis vermis*). St. Girons (1964) suggested 2 weeks as the probable interval between ovulation and egg deposition in the sea snake *Laticauda colubrina*. Tinkle (1967) reported an average of about 2 weeks for oviductal egg development in the lizard *Uta stansburiana*. Numerous reports exist of time elapsed between mating and egg-laying, but these cannot be used as measures of time from ovulation to egg deposition because of uncertainties concerning the temporal relationship between mating and ovulation. The observation by Minton (1966) on the snake *Spalerosophis atriceps* in Pakistan is informative in this regard. The time between mating and egg deposi-tion by the same captive female in 2 different years was 77 days and 18 days!

There is at least an indication that egg-guarding species may have slightly shorter development times than those that do not guard eggs

TABLE 14
GESTATION PERIODS OF VIVIPAROUS LIZARDS AND SNAKES

	SPECIES	FAMILY	GESTATION PERIOD	REFERENCES
1.	*Lacerta vivipara*	Lacertidae	38–65 days (usually > 50)	Panigel 1956
	Lacerta vivipara	Lacertidae	about 90 days	Fukada 1965
2.	*Sceloporus cyanogenys*	Iguanidae	52 days	Hunsaker 1959
3.	*Egernia striolata*	Scincidae	about 2 months	Bustard 1970b
4.	*Anguis fragilis*	Anguidae	about 2 months	Rollinat 1934
5	*Virginia striatula*	Colubridae	60–90 days	Clark 1964
6.	*Phrynosoma douglasi*	Iguanidae	about 3 months	Goldberg 1971
	Phrynosoma douglasi	Iguanidae	68–82	Nussbaum (pers. comm)
7.	*Sistrurus catenatus*	Crotalidae	70–90 days	Keenlyne 1968
8.	*Gerrhonotus coeruleus*	Anguidae	10–12 weeks	Vitt 1973
9.	*Vipera berus*	Viperidae	2½ months	Volsoe 1944
10.	*Agkistrodon piscivorus*	Crotalidae	approx. 2½–3 months	Wharton 1966
	Agkistrodon piscivorus	Crotalidae	approx. 3½–4 months	Burkett 1966
11.	*Leiolopisma zeylandica*	Scincidae	12–13 weeks	Barwick 1959
12.	*Thamnophis sirtalis*	Colubridae	87–116 days	Blanchard and Blanchard 1941
	Thamnophis sirtalis	Colubridae	Approx. 100 days	Fitch 1965
13.	*Thamnophis butleri*	Colubridae	89-102 days after mating (zoo records)	Fitch 1970

	Species	Family	Gestation	Reference
14.	*Xantusia vigilis*	Xantusiidae	3 months (field & lab)	Miller 1951, 1954
15.	*Sphenomorphus quoyi*	Scincidae	about 3 months	Veron 1969
16.	*Natrix rhombifera*	Colubridae	90 days	Betz 1963
17.	*Vipera aspis*	Viperidae	3 months	St. Girons 1957
18.	*Agkistrodon contortrix*	Crotalidae	105–110 days	Fitch 1960
19.	*Storeria dekayi*	Colubridae	approx. 110 days after mating	Clausen 1936
20.	*Anniella pulchra*	Anniellidae	about 4 months	Miller 1944
21.	*Hemiergis peronii*	Scincidae	about 4 months	Smyth & Smith 1968
22.	*Coronella austriaca*	Colubridae	about 4 mos. after mating	Fitch 1970
23.	*Crotalus ruber*	Crotalidae	141–175 days after mating	Fitch 1970
24.	*Sceloporus malachiticus*	Iguanidae (TR)	Approx. 5 months	Marion and Sexton 1971
25.	*Liolaemus multiformis*	Iguanidae	Minimum of 5 months (winter)	Pearson 1954
26.	*Sceloporus jarrovi*	Iguanidae	6 months	Ballinger 1973
26.	*Sceloporus jarrovi*	Iguanidae	6 months	Goldberg 1971
27.	*Epicrates striatus*	Boidae (TR)	about 6–7 months	Fitch 1970
28.	Sea snakes (six species)	Hydrophiidae (TR)	about 6 months	Bergman 1943
29.	*Sceloporus poinsetti*	Iguanidae	7 months (winter)	Ballinger 1973
30.	*Corytophanes percarinatus*	Iguanidae (TR)	6–7 months	McCoy 1968

(Fig. 1). However, many egg-guarding species reportedly lay eggs in an advanced state of embryonic development. In fact, the frequency of egg retention prior to oviposition by egg-guarding species is one phenomenon that makes egg-guarding an appropriate subject in our discussion of the evolution of viviparity. Egg-guarding does not appear to be more common in temperate than in tropical species (Fig. 1).

If cold environments engender long development times, intra-specific latitudinal variation in incubation times might be expected for wide-ranging species, with longer periods in the colder regions. Unfortunately, geographic and intrapopulational variation in incuba-tion times is known from little more than anecdotal information. Eggs of the ringneck snake (*Diadophis punctatus*) from Michigan varied in incubation time in the lab from 58-84 days (Blanchard, 1930). The lower figure was for eggs maintained at warm tempera-tures and the higher one for eggs maintained under cool conditions. The average incubation time for this species in Kansas was reported by Fitch (1975) to be 60 days in the lab. Blanchard (1933) reported an incubation time averaging 2 weeks for 41 clutches of eggs of the smooth green snake (*Opheodrys vernalis*) in Michigan. Stille (1954) recorded a mean hatching time of one month for 28 eggs of this species in the Chicago area. Among the eggs of the racer (*Coluber constrictor*), incubation periods in Kansas varied from 43-63 days (Fitch, 1963a). The record incubation period recorded by Fitch was 73 days for eggs of this species in Texas. Bechtel and Bechtel (1958; 1962) reported that incubation times for eggs of the corn snake (*Elaphe guttata*) in the lab varied from 73-97 days. The locality from which their snakes came is unknown, but these periods are longer than those reported for eggs of this species in Florida (57-63 days) by Holman (1960) and MacMahon (1957). These scant data allow no conclusion concerning the relationship between latitude and incuba-tion time.

Before meaningful latitudinal comparisons between populations can be made, the variation within populations of a species must be known. The following reports demonstrate that this period can be extremely variable. Fitch (1954) recorded egg incubation times of 27-47 days in the skink *Eumeces fasciatus* depending upon the incubation temperature; the longer periods were observed under cooler conditions. Hecht (1930) reported that *Natrix natrix* in Europe retained eggs under conditions unfavorable for deposition. In such instances, the period of development after laying was shortened from an average of 60 days to as few as 30. In the lizard *Crotaphytus collaris*, Fitch (1956) reported that approximate periods of incuba-tion in nature varied from 52-94 days. Platt (1969), who studied the hog-nose snake (*Heterodon nasicus*) in Kansas, cited several examples of 50-60 day incubation periods for eggs of this species in the lab, but eggs of one clutch at fairly cool temperatures (74°F) averaged 81

days in incubation. Table 13 shows that 50% differences between minimum and maximum incubation times are common within species and 100% differences are occasional. The most extreme differences between minimum and maximum incubation periods are the 29-76 days reported for the fence lizard (*Sceloporus undulatus*), 35-88 days in the green snake (*Opheodrys aestivus*), 46-160 days in the wall lizard (*Lacerta muralis*), and 85-207 days in the gecko (*Phyllodactylus marmoratus;* Table 13).

In many instances, temperature can be shown to alter dramatically the period of development. Such lability in development time within a species makes exceedingly difficult comparison of incubation times of species in different geographic areas with data currently available. For this reason, interpretations based on data presented in Table 13 and Figure 1 should be treated with caution. A further difficulty is that the data themselves are often not comparable. In some instances the incubation times are estimated from the field, usually as the period from when the first females with oviductal eggs appear to the time when the first hatchlings are observed. In other cases, the incubation times are determined under laboratory conditions. Frequently, the temperature at which incubation actually occurs in nature is unreported or unknown. Too, many reports on incubation times are based on one or a few eggs or clutches and without knowledge of that part of the egg development that occurred in oviducts prior to egg deposition. Genetic differences in rates of post-ovipositional egg development presumably occur within and among species but such differences will not be clearly demonstrable until numerous studies have measured incubation periods under comparable experimental regimes. One example of apparent genetic difference in incubation time within a species is that of *Gehyra australis* in which eggs from two different population incubated under the same temperature conditions hatched in dramatically different periods of time (74-101 days vs. 139-148 days: Bustard, 1969a). Interestingly, eggs from the cold temperature population had the shorter incubation times, when all eggs were kept at the same temperature. It would be particularly instructive to study embryonic development times between eggs from populations that occupy quite different climatic regimes within the same wide-ranging species of reptiles. We would expect that development times would be longer in the eggs from high latitude populations but that under the same experimental temperature conditions, development times at high temperatures should be faster for the warm-adapted eggs and development times at low temperatures should be faster for the cold-adapted eggs. Thus we would expect adaptation in developmental physiology to compensate for temperatures; however, such adaptation need not totally obliterate differences in natural development times at different latitudes within a species; furthermore, rapid development if adaptive in a cold environment ought also to be so in

a warm one, particularly in a viviparous species. These considerations further indicate the necessity for carefully controlled studies of reptile development. The most nearly comparable data for comparing incubation and gestation periods between species should come from species occupying the same geographic area. Such are available for several species of snakes and lizards studied by Fitch and his associates in a local area of Kansas. The data available for 11 egg-laying species (Table 13, Nos. 34, 36, 41, 46, 52, 55, 71, 76, 78, 82, 112) and 2 viviparous ones (Table 14, Nos. 12 and 18) show that the incubation period of egg-layers varies from 42-75 days among lizards and 50-60 days among snakes. The two viviparous snake species, in contrast, each requires more than 100 days to complete gestation. Most viviparous squamate species at latitudes comparable to that of Kansas have equally long gestation periods (Table 14). Even allowing for some period of intrauterine retention of eggs prior to deposition in the oviparous species, the gestation periods of the viviparous ones still seem long by comparison.

Most lizard species may be capable of retaining the eggs for short periods of time prior to deposition (Sexton and Marion, 1974). However, exceedingly short incubation periods are characteristic of some species; thus, intrauterine development prior to oviposition as a species characteristic is as widespread a phenomenon in reptiles as viviparity itself (Tables 13, 14). Reptiles such as *Eumeces callicephalus* among lizards and *Opheodrys vernalis* among snakes presumably represent cases of intermediacy between oviparity and viviparity in which most of the embryonic development occurs prior to egg deposition.

DISCUSSION

Factors Correlated with Viviparity

The correlation most cited is that between cold environments and the proportion of viviparous species in the squamate fauna. The data presented here on the latitudinal and altitudinal distribution of squamates support previous conclusions by Sergeev (1940) that the proportion of viviparous species in the total reptile fauna increases as one moves toward the poles or to high elevations. However, several problems arise in attempting to infer causality from this correlation. Proportions can be misleading because far northern or southern and high altitude reptile faunas are exceedingly impoverished: for example, only a single species (*Bothrops ammodytoides*) reaches extreme southern South America. One or a few viviparous species in an impoverished fauna have enormous proportional representation as can be readily seen for the higher latitude zones of the United States (Table 2). We feel that an explanation for the evolution of viviparity should also consider those situations in which the majority of

viviparous species occur. In North America the absolute numbers of viviparous species increase monotonically as one proceeds south, not as one proceeds north. A southern state such as Alabama has 20 viviparous species of snakes, twice the number that exist in Michigan and four time as many as exist in southern Canada above 50° north latitude. This is in contrast to the high proportion (above 60%) of viviparous squamates in southern Canada. The same pattern of absolute numbers of egg-laying and live-bearing species occurs at comparable latitudes in Australia. Thus as one goes south from latitude zone 30°-35°, into more temperate climates, the numbers of both oviparous and viviparous species decline. Similar patterns of decreasing numbers of reptile species, both oviparous and viviparous, may occur with increases in elevations, but studies to date are too few to clearly delineate these patterns.

The association of viviparity with cold environments has been made repeatedly by examining species with extreme distributions near the limits of the geographical or altitudinal range for all reptiles. For example, in Europe *Lacerta vivipara* and *Vipera berus* are frequently cited as cases of live-bearing species reaching very high latitudes, even above the Arctic Circle. That numerous egg-laying species exist at high latitudes or altitudes has sometimes, seemingly, been overlooked. For example, the egg-laying snake *Natrix natrix* reaches 65° north latitude (Darlington, 1957). Furthermore, North American squamates with most of their ranges occurring above the 40th parallel or at high altitudes (Table 5) are almost equally represented by egg-laying and live-bearing species. If viviparity were primarily an adaptation to cold environments, species endemic to cold regions would be expected to show an especially high frequency of viviparity. Instead, the proportion of viviparous species in this northern faunal element is not substantially different from that for all U.S. species that reach above 40°N latitude (Table 2).

We emphasize the point that among reptiles, regardless of reproductive mode, the number of species declines as one progresses toward the poles or to higher elevations. At the extremes of latitude and altitude, the reptile fauna is often represented mostly or entirely by a few viviparous species. This suggests only that viviparous species, once they reach such localities, are able to survive better than oviparous ones. But this small contingent of the world's viviparous squamate fauna should be used with caution in arguing that temperature was the prime selective pressure leading to viviparity in the first place. A similar thought may have occurred to Greer (1967a): "It has undoubtedly been live-bearing habits that have enabled anguids (along with live-bearing iguanids and scincids) to play such an important role in the high altitude reptile fauna of Mexico and Central America." We re-emphasize the need for comparative studies of the latitudinal and altitudinal distributions of genera having both oviparous and viviparous species. If systematists familiar with these genera could

demonstrate that the viviparous species therein represent descendants
derived from the more diverse oviparous fauna of milder climates, this
would provide a more convincing argument that viviparity initially
evolved in response to colder conditions.

Thus far, only the correlation between viviparity and cold
environments has been discussed in detail. However, Mell (1929),
Sergeev (1940), Neill (1964), Packard (1966), and Fitch (1970) have
all hypothesized that other traits, such as arboreal or burrowing
habits, restriction to aquatic or xeric environments, and venomous-
ness, may enhance selection for viviparity. These hypotheses have
been erected to explain viviparity in particular kinds of species but
do not seem to have general applicability. Table 15 lists the ecological
correlates with viviparity suggested by Neill (1964) and Fitch (1970)
and the species mentioned by them to exemplify the correlation with

TABLE 15

EXAMPLES OF VIVIPARITY AND OVIPARITY IN SELECTED REPTILES
OCCURRING IN PARTICULAR ENVIRONMENTS OR HAVING CERTAIN
LIFE STYLES[1]

LIFE STYLE	VIVIPAROUS	OVIPAROUS
High latitude (cool climate)	*Coronella* — FN *Elaphe* — F *Heteropholis* — F *Hoplodactylus* — F *Lacerta* — F *Naultinus* — F *Trimeresurus* — N *Vipera* — N	*Coluber constrictor* *Diadophis punctatus* *Elaphe vulpina* *Eumeces fasciatus* *Eumeces septentrionalis* *Heterodon nasicus* *Lacerta agilis* *Lampropeltis triangulum* *Natrix natrix* *Opheodrys vernalis* *Pituophis melanoleucus*
High elevation (cool climate)	*Conopsis* — F *Corytophanes* — F *Crotalus* — N *Liolaemus* — F *Phrynosoma* — F *Sceloporus* — F *Thamnophis* — N *Toluca* — F	*Algyroides alleni* *Gerrhonotus kingi* *Lacerta agilis* *Lampropeltis zonata* *Liolaemus monticola* *Natrix nuchalis* *Sceloporus aeneus* *Trimeresurus monticola*
Arboreal	*Ahaetulla* — F *Cophotis* — F *Thamnodynastes* — N	*Anadia* *Anolis* *Chrysopelea* *Dendrelaphis* *Draco* *Imantodes* *Oxybelis* *Ptychozoon* *Rhampholeon*

TABLE 15 (continued

LIFE STYLE	VIVIPAROUS	OVIPAROUS
Marine or aquatic	*Acrochordus* — FN *Helicops* — F Homalopsinae — FN Hydrophiinae — FN Natricinae (New World) — N	*Boulengerina* *Grayia* Laticaudinae *Lycodonomorphus* Natricinae (Old World) *Tretanorhinus*
Xeric habitat	*Egernia* — F *Hemiergis* — F *Phrynocephalus* — F *Sphenomorphus* — F *Tiliqua* — F *Trachydosaurus* — F	*Chionactis* *Moloch* *Phyllorhynchus* *Pseudocerastes* *Sauromalus* *Uromastix*
Poisonous	*Acanthophis* — F *Agkistrodon* — F *Bitis* — F *Bothrops* — F Crotalidae — N *Crotalus* — F Elapidae (Australia) — N *Haemachatus* — F, N *Notechis* — F *Trimeresurus* — F *Vipera* — F Viperidae — N	*Agkistrodon rhodostoma* *Bungarus* *Causus* *Demansia* *Dispholidus* *Echis colorata* *Heloderma* *Lachesis* *Micrurus* *Naja* *Oxyuranus* *Trimeresurus flavoriridis*
Fossorial; highly secretive	Cordylidae — F Xantusiidae — F *Xenosaurus* — F	*Bachia* *Calamaria* *Farancia* Leptotyphlopidae *Neoseps* *Nessia* *Ophisaurus* Typhlopidae

[1]The genera and families listed in the viviparous column were used as examples by Fitch (1970; = F) or Neill (1964; = N) to represent species which had adopted viviparity in correlation with a particular ecological or morphological life style. The other column contains our selected oviparous counterexamples to these.

a particular environment or life style. We counterpose an array of oviparous reptiles which would support a contention that oviparity also was correlated with these same independent variables. This exercise is not meant to disparage these authors, but only to point out that the approach of selectively choosing examples may not lead to generality. However, we recognize that indeed there may not be a single, general hypothesis that suitably explains every case of vivi-

parity. Nevertheless, we feel that these ecological correlates are less likely to have been causative factors in the transition from oviparity to viviparity than were cold temperatures.

Phylogenetic Constraints on Viviparity

Some authors (for example, Neill, 1964; Fitch, 1970) have suggested that viviparity, once evolved, is irreversible. One implication of such a phylogenetic constraint is that some species are viviparous because of their ancestral lineage, not because of an adaptation to their immediate environment.

This argument of irreversibility is basic to the oft-cited case of the distribution of reproductive habits among the watersnakes (*Natrix* sensu latu; see Rossman and Eberle, 1977) of the New and Old World. Thus, the conventional argument is that New World *Natrix* (or more broadly, natricines) are universally viviparous because only a cold-adapted viviparous ancestor could have crossed the Bering Strait from Asia (Malnate, 1960). Consequently, the diverse New World natricines are viewed as viviparous because of this viviparous common ancestor and the assumed irreversibility of viviparity. If one accepts the idea of such a phylogenetic constraint on the evolution of reproduction in New World natricines, the question still remains of why the maximal diversity of these species is not at higher latitudes. This present pattern could be explained by the commonly accepted thesis that viviparity evolved in the north and was followed by a migration southward and rapid speciation of natricines there. An alternative hypothesis is that the evolution from oviparity to viviparity actually occurred in the southern U.S. in response to certain conditions there, with subsequent speciation and migration of some species to the north. This latter hypothesis would not invoke cold conditions as the primary selective force leading to viviparity, but would require a southern origin for northern U.S. natricines and would also raise the question of why there are no oviparous species in the southern U.S.

However, in view of the universality of viviparity in North American natricines it is parsimonious to assume that they did have a viviparous common ancestor. But it is not necessary to assume that the ancestor was viviparous prior to entering North America. Literature on Old World *Natrix* suggests to us that egg-laying forms occur commonly in fairly cold environments. *Natrix annularis,* the only live-bearer, occurs only at low to moderate elevations. In contrast, many of the oviparous species occur at high elevations and northern latitudes and many are noted by Pope (1935) to be restricted to elevations above 5000 feet. Thus, many of the oviparous Asiatic *Natrix* are presently living in cool montane environments and could seemingly have readily reached North America by way of the Bering Strait if cold climatic conditions were the major barrier to dispersal.

Other possible evidence of phylogenetic constraint might be the universal viviparity in some reptile families, both lizards (*Anniellidae, Xenosauridae* and *Xantusiidae*) and snakes (*Uropeltidae* and *Acrochordidae*). Also, a high proportion of viviparity in other taxonomic groups could be indicative of irreversibility. Greer (1968b) reported 30% viviparity among the 243 skink species of known reproductive habits. Greer (1967a) likewise reported a very high frequency of viviparity among anguid lizards. That viviparity may not always be irreversible could be indicated by the egg-laying pit viper (*Lachesis muta*) in Central and South America which is the only oviparous crotalid snake in the New World. This species could, of course, represent the primitive oviparous ancestry of the viviparous pit vipers but this seems less likely in view of Brattstrom's (1964) study showing that *L. muta* possesses many advanced pit viper characteristics.

The fact that viviparity occurs in so many unrelated groups (Table 11) suggests that a transition from oviparity to viviparity has been relatively frequent in phylogeny and that the transition may have been fairly simple genetically. In contrast, the rarity of intraspecific bimodality seems paradoxical. The occurrence of egg-retention, presumably an intermediate stage between oviparity and viviparity, is widespread in otherwise normally oviparous species. However, at some point in the evolution of viviparity, presumably *after* complete development of the young within the mother has occurred, loss of shell glands or enzymes necessary for shell production may make reversion to oviparity difficult or impossible for descendants of those species. A transition from viviparity to oviparity is less likely than the reverse because going from oviparity to the initial stages of viviparity primarily involves loss of structure or function. Going from viviparity to the initial stages of oviparity, on the other hand, requires additions such as shell glands. If viviparity is difficult to reverse within species then an explanation for the rarity, both in absolute numbers and proportions, of viviparous species of reptiles in the tropics suggests itself. Many tropical species are capable of producing multiple clutches. Viviparity within a species, therefore, could represent a great competitive disadvantage compared to oviparity in the tropics because such reproductive habits could restrict potential fecundity by greatly limiting the number of litters per year. We do not imply that fecundity is the only determinant of fitness, but it may be one of the most important when comparing multiple-brooded oviparity with the likelihood of single-brooded viviparity.

Developmental Times and Egg-Retention: Intermediate Stages Between Oviparity and Viviparity.

Our compilation of data on incubation and gestation (Tables 13 and 14) in no way supports the idea implicit in Sergeev (1940) that

viviparous species have shorter developmental periods than egg-layers. We recognize that he may have meant that viviparous species had shorter developmental periods than they would have had if they had remained oviparous. However, the limitations of the data are sufficiently serious to require that certain studies be conducted before meaningful comparisons can be made. The following seem particularly relevant:

1) Time of ovulation and length of period of oviductal egg-retention in oviparous species.
2) Gestation period from ovulation to birth in viviparous species.
3) Relation between actual body temperatures and length of the gestation period.
4) Relation of incubation times in natural nests to environmental temperatures.
5) Relative incubation times of eggs and gestation periods of embryos from climatically different parts of the range of a species maintained under identical lab conditions.

The study of Sexton and Marion (1974) using controlled incubation temperatures for eggs of *Sceloporus undulatus* is exemplary in this regard. However, additional studies of developmental times of reptiles under lab conditions at unknown temperatures are of very little value. Likewise, incubation times of reptile eggs collected under natural conditions but of unknown age, such as reported by Pongsapipatana (1975), are of dubious value.

If environmental temperatures in the tropics are warmer and more constant than those in most temperate areas, we would expect developmental periods to be noticeably shorter there. However, Figure 1 offers no support for this contention. The variance in incubation times appears to be greater for tropical species. Although it is possible to suggest reasons for such patterns of development, including the possibilities that incubation temperatures are not actually warmer in the tropics or that selection for shorter developmental periods in egg-layers is less stringent, we are reluctant to do so because of the previously discussed limitations of the data.

Table 13 and Figure 1 indicate the enormous variance that exists in post-ovipositional incubation time. The shortest incubation time, however, does not necessarily reflect a faster rate of embryonic development but, instead, may be indicative of a retention of the eggs *in utero* with resultant variable degrees of embryonic development among species prior to egg deposition. Such egg-retention may be viewed as an intermediate step from oviparity to viviparity exactly as hypothesized by Sergeev (1940). Therefore, species having such intermediate stages ought to be most frequent in the same environments in which viviparous species are most common. Table 16 lists several species known to lay eggs with embryos partially developed. The majority are temperate with only three being from the low

TABLE 16

EXAMPLES OF REPTILES HAVING WELL-DEVELOPED
EMBRYOS AT THE TIME OF EGG LAYING[1]

Python (most species)	Fitch 1970
Dendrelaphis	Smith 1943
Typhlops schlegeli	FitzSimons 1962
Elaphe dione	Pope 1935
Opheodrys vernalis	Blanchard 1933
Tretanorhinus variabilis (inferred)	Petzold 1967
Natrix (=Amphiesma)vibakari (inferred)	Fukada 1965
Saiphos equalis	Cogger 1975
Psammophylax rhombeatus	FitzSimons 1962
Pseudocerastes fieldi	Mendelssohn 1965
Agkistrodon acutus	Pope 1935
Trimeresurus monticola	Pope 1935
Liolaemus monticola	Fitch 1970
Sceloporus virgatus	Vinegar 1975
Eumeces callicephalus (inferred)	Zweifel 1962
Natrix stolata	Pope 1935
Zaocys dhumnades	Pope 1935
Lacerta agilis	Rollinat 1934
Agkistrodon rhodostoma	Smith 1943
Typhlops diardi	Wall 1918; Smith 1943
Diadophis punctatus	Fitch 1975
Sceloporus clarki	Stebbins 1954
Sceloporus scalaris	Anderson 1962; Newlin 1976
Helicops angulatus	Rossman 1973

[1]Inferred in parentheses means that we have made the inference on the basis of published incubation periods.

elevation tropics. These data suggest that egg-retention is most common in temperate latitudes and could support the hypothesis that viviparity is an adaptation to cold, but the data may be biased because the reproductive habits of tropical species are less well known.

The fact that some species are able to retain their eggs until development is nearly complete suggests that the final transition to viviparity may require relatively small genetic changes. The elaborate placentation evolved in some species (Weekes, 1935) is not a necessary concomitant of viviparity but a later specialization. Blanchard (1933) stated that the reduction of the period of development after egg-laying in the smooth green snake to as few as four days "suggests the possibility of occasional ovoviviparity in this species." Such a species as this would be a prime subject to determine if viviparity could be induced experimentally and if individual plasticity in reproductive mode occurs. Rossman (1973), likewise, has suggested that individual plasticity in reproductive mode may occur in *Helicops angulatus.* Weekes (1935) and Packard (1966) have both suggested

that the importance of the egg shell could limit the transition from oviparity to viviparity in nature. Weekes (1935) stated (p. 641) that it was difficult to conceive of viviparity evolving in dry environments because the intermediate steps from oviparity to viviparity would have resulted in progressively thin-shelled eggs particularly subject to dehydration. Packard (1966) made a similar argument (p. 674): "reptiles that were experiencing an evolutionary loss of the egg shell, thereby permitting longer periods of uterine development, could not have laid their eggs—even eggs in terminal stages of development—in an arid environment . . . " Neill (1964) perhaps should be credited with pointing out one error in such thinking; the first steps toward viviparity could involve progressively longer retention of the eggs in the body of the female "so that a live-bearing condition is approximated before thinning of the egg shell begins." We further add that thinning of the egg shell is not a necessary intermediate stage between oviparity and viviparity. All that is required is that shell deposition be delayed until later and later in development and finally suppressed altogether. Once the exact time of shell deposition in species with very short incubation times is ascertained, we predict that it will be found to occur late in embryonic development immediately prior to egg deposition. If so, it is unnessary to view thinner shelled eggs as an essential intermediate step in the evolution of viviparity.

Egg-Guarding as an Alternative to Viviparity

Many species reported to retain eggs during part of embryonic development also guard them after they are laid. For this reason, we included egg-guarding species in this paper (Table 13; Fig. 1). Egg attending may extend throughout incubation as is true of most North American skinks, or it may be terminated after a short period (*Elaphe quadrivirgata;* Fukada, 1965). Attendance of the young may even continue for a short time after hatching (Evans, 1959). Although we use the term egg-guarding (as did Neill, 1964), we emphasize that actual guarding of the eggs in a defensive or offensive sense has seldom been documented, nor has the habit of egg-guarding ever been satisfactorily explained. Fitch (1970), for example, simply states that it may be an alternative to or a substitute for viviparity. Neill (1964) argued that egg-guarders obtain one advantage of viviparity (care of the eggs) without incurring the disadvantages of carrying them around within the mother. In this sense egg-guarding can be viewed as an alternative to viviparity. However, at least three major questions remain:

1) What evolutionary steps have actually led to egg-guarding?
2) Why is egg-guarding evidently so rare among reptiles?
3) Why should egg-guarding species remain oviparous rather than becoming viviparous?

In addressing the first question it seems most parsimonious to assume that egg-guarding arose incidental to the association of a female with her eggs. Remaining with the eggs could arise in environments in which resources for the adult, at about the time of egg deposition, become increasingly scarce or unpredictable so that searching for such resources could be a high risk endeavor. Then, if the site chosen for egg deposition were particularly favorable as a hiding place or refugium for the female, such that remaining there lowered her mortality risk, a female remaining with her eggs for longer periods could be favored over those abandoning their eggs after deposition. Active egg-guarding could then develop from this passive association of female and eggs because the greater survivorship among eggs of parents attending them and offering some form of protection compared to those not so doing could result in much higher fitness of egg-guarding parents relative to non-guarders. This could be particularly true among large and poisonous species in which these egg-guarding habits do seem more common. One additional form of protection, applicable to all species, could be that of removing dead eggs which might attract predators or serve as a source of contamination or infection to the others. We thank Harry W. Greene for informing us of his observations of *Gerrhonotus lio-cephalus* in which a nest-guarding female apparently removed spoiled eggs from the nest.

In environmental situations in which resources are not scarce or unpredictable at the time of egg laying, parents remaining with eggs could be at a disadvantage because of a potential restriction on fecundity due to limitations of resource exploitation. We assume this type of environmental situation to be the one with which reptiles are most commonly confronted.

To the question of why egg-guarding species do not become viviparous, Neill (1964) has supplied one possible answer. He suggested that an egg-guarding female is more capable of rapid escape than is a viviparous female burdened with young. We also suggest that a guarding female (relative to a strictly viviparous one) is able to gain sufficient resources to begin production of a second clutch of eggs whereas that might not be possible or might incur too high a cost in a viviparous parent. The female's effectiveness in seeking prey resources would of course be dependent upon her faithfulness to the nest. However, such resources could come, in part, from eating predators attracted to the nest.

In summary, we suggest that females of egg-guarding species will be found to produce more clutches of eggs per season (relative to related viviparines in similar habitats), will have very low mortality while remaining with the eggs, or will most often be found in environments where resources for adults are limited at the time of egg deposition. Finally, as implied by Trivers (1972), males in polygynous species with internal fertilization can be less certain of

their paternity than females can be of their maternity and are therefore less likely to devote parental care to their eggs or young. Therefore, we predict that egg-guarding by males will be found rare or non-existent in reptiles.

A General Theory of the Evolution of Viviparity in Reptiles

Obvious advantages are apparent for either of the two extreme reproductive modes, viz. oviparity and viviparity (Table 1). To understand the transition from one mode to another, we must be able to visualize how intermediate conditions, obviously common among living reptiles, could be adaptive.

Sergeev (1940) has stated particularly clearly one hypothesis to explain the correlation that exists between cold conditions and viviparity. He emphasized the potential for thermal regulation of development by viviparous species in cold environments and that viviparous species might avoid the higher probability of mortality of the eggs that could result during the longer developmental periods that would presumably accompany oviparity. However, the data we have presented do not suggest rapid development times in high latitude viviparous species when compared to sympatric oviparous species.

An alternative and complementary explanation for the adaptiveness of egg-retention and viviparity is that, rather than being mechanisms for thermo-regulation, these allow embryonic development to proceed within the mother but also allow her the option of holding eggs until environmental cues indicate that conditions for egg-laying are optimal. Species with a previous history of evolution in more equable environments, but whose expanding geographic range brings them into much more variable ones, such as those at high latitudes, would presumably experience difficulty in predicting, at the time of egg deposition, whether the site chosen would remain favorable throughout the period of incubation and early life of the hatchlings. In such environments selection might favor females which held their eggs through some part of this period of developmental uncertainty. Cold environments may exacerbate this problem of predictability by increasing the length of the incubation period and making it less likely that the egg deposition site chosen by the parent will remain favorable until and after hatching. The more unpredictable the environment (whether for reasons of climate, predation, or resource availability) of the eggs and hatchlings the more likely that the complete transition to viviparity will be favored by selection because egg-retention until birth allows the female the maximal option in selecting the most propitious time and place for the birth of her young. The environmental variability of the temperate regions thus

may provide strong selective pressures for egg-retention and for the evolution of viviparity.

We noted above the necessity for explaining the persistence of intermediate stages between oviparity and viviparity as evolutionarily stable strategies. The longer a female must carry developing young the longer she must incur the associated risks and higher maintenance costs. Also, the longer the period of pregnancy, the less likely is the initiation of a second clutch. Thus, a female would be expected to carry young only until there is high probability of placing them in a favorable site. It seems particularly difficult to understand instances like that of *Opheodrys vernalis* in which the female carries the eggs most of the way through development, only to deposit them with two or three weeks of incubation time remaining. However, if the probability of egg survivorship is essentially assured by egg-retention through most of the uncertain developmental period, then it could be disadvantageous for a female to carry eggs all the way to term. This would be true if those females depositing their eggs slightly earlier than those holding them to term held the advantages of more effective exploitation of resources and avoidance of some mortality sources. In short, the risks acceptable to a female early in the period of egg-retention may become too costly late in the developmental period once survivorship of the eggs becomes more assured; if true, then it is not surprising that all cases of egg-retention do not lead ultimately to viviparity. Perhaps in some years females that do carry eggs to term may be favored so that plasticity of reproductive habit becomes characteristic of the species. That such plasticity may occur in *Opheodrys vernalis* has been suggested by Blanchard (1933), but never substantiated for this or any other species in nature.

Temperate environments restrict the length of the reproductive season, leading to predominantly single-brooded species as discussed in detail by Tinkle (1969). Furthermore, Tinkle, Wilbur, and Tilley (1970) noted the association of viviparity with single-broodedness. Viviparous reproduction presumably entails a cost to adult survival and fecundity and a presumed gain in survival of young, relative to oviparous reproduction. The gain in juvenile survivorship may not offset both the cost of adult mortality and the cost of reduced fecundity, if multiple clutches are possible. In a variable environment multiple clutches also can be advantageous because the probability of having a successful clutch is increased. However, in environments with shorter breeding seasons such as those at high latitudes, the selective balance may be in favor of single-broodedness, egg-retention, or viviparity rather than multiple-broodedness.

Snakes in cooler regions of the world are almost invariably reported to be single-brooded, an interesting fact for which we attempt no explanation. Lizards, on the other hand, are less often single-brooded (Tinkle, et al 1970). Therefore, we are not surprised that viviparity also is more common among snakes than among

lizards. Sergeev (1940) was the first to mention that the frequency was higher among snakes, and this fact has been clearly documented here (Tables 2, 3, 6, and 7).

In contrast to the situation in temperate regions, the potential loss in fecundity incurred by viviparous modes compared to multiple-brooded oviparous ones can be enormous in tropical environments or in those temperate areas which have long seasons favorable for reproduction. As expected, data for several tropical regions (Tables 6, 7, 8) indicate viviparity in only 20 of 215 lizard species (9.3%) and 73 of 447 snakes species (16.3%). These proportions and absolute numbers are much lower than encountered in temperate regions. These data also indicate that even in the tropics viviparity may be more common among snakes than among lizards.

Greene (1970) recognized the difficulty of explaining the dearth of viviparous species among tropical snakes: "It is of course possible that there simply has not been sufficient selection pressure to favor the widespread evolution of viviparity (in the tropics), but this does not explain why they have not been invaded by species which have already developed live-bearing habits." We think that in general viviparous, compared to multiple-brooded oviparous, reptiles are at a disadvantage in the tropics because of the reduced fecundity associated with carrying young. If true, this could explain why viviparity rarely evolves in the tropics, and why so few temperate viviparous groups invade the tropics. We recognize that this hypothesis suggests that in areas with long reproductive seasons multiple-broodedness ought to exist among egg-laying species of snakes although, unlike the situation in lizards, this has been rarely reported. We think these data deficits are partly attributable to the lack of detailed knowledge of the reproductive cycles of nearly every species of snake. Nevertheless, reports of more than one reproduction in a season are available for a few egg-laying and viviparous species. Some of these reports are based on lab research and include the following snake species (from Fitch, 1970): oviparous—*Causus rhombeatus, Pituophis melanoleucus, Ptyas korros, Ptyas mucosus, Boiga multimaculata;* viviparous—*Regina alleni, Seminatrix pygaea, Thamnophis proximus,* and *Thamnophis sauritus.* Saint Girons and Pfeffer (1971) listed nearly a dozen Cambodian snakes that produce more than one annual litter in nature. Numerous other species have been reported to have reproductive seasons sufficiently long to allow production of two or more clutches or litters.

The absence of viviparity in turtles and crocodilians seems puzzling, particularly in view of the documented high nest mortality in some species of the former. We could invoke the explanation of Williams (1966) for birds that they simply lack some necessary preadaptation for viviparity. But it is difficult to understand why these groups have been constrained given the phylogenetic antiquity of viviparity. One explanation for the turtles is that viviparity could be disadvantageous because of the attendant reduction in fecundity.

The generally omnivorous diets of most species provide them with a wide range of food resources which may allow production of more than one clutch of eggs in a season. If this interpretation is correct, then it is not surprising that multiple clutches have been documented for many species of turtles, even in the northern parts of their range (Ernst and Barbour, 1972). Furthermore, in the case of aquatic and marine turtles, eggs are laid in an environment removed and quite different from the one in which they live. Therefore, retention of the eggs in the oviducts may be ineffective as a means of increasing the probability of later placing them in the most optimal environment. A female which attempted to insure such predictability would need to leave the water more frequently to gauge the suitability of the terrestrial environment for egg deposition. This would presumably increase her risk of predation, seemingly an unacceptably costly behavior considering the otherwise long life expectancy with frequent opportunities for nesting. Finally, most early mortality in turtles is reported to occur on eggs in the nest no matter when laying occurs; therefore, little is to be gained from retention of eggs for variable lengths of time. This initial stage in the transition from oviparity to viviparity seems less likely to be adaptive in turtles than in some squamates.

The absence of viviparity in the fewer than two dozen species of crocodilians does not seem difficult to explain. For one thing all species are restricted to tropical or warm-temperature climates, and hence have the potential for higher fecundity through oviparity. However, we are unaware of examples of multiple-brooding among tropical crocodilians. Also, egg-guarding, a frequently documented trait among crocodilians, may have been favored as an alternative to viviparity for reasons given earlier for large and dangerous squamates.

Whether or not our comments pertaining to turtles and crocodilians are compelling, we feel certain that the recent hypothesis by Packard et al (1977) to explain the absence of viviparity in these groups is untenable. In brief, they argued that the reliance of the embryos on calcium from the egg shell precluded the reduction in shell thickness necessary for intrauterine gaseous exchange which would be required for the prolonged retention of embryos. Such a physiological constraint on the evolution of viviparity seems unlikely, because were viviparity advantageous surely some alternate mechanism of calcium storage and metabolism could be utilized as has been demonstrated for squamate reptiles by Jenkins and Simkiss (1968). In particular, it is not clear why the parent could not simply delay shell deposition in the eggs with the prospect of later deposition to its embryo. In other words, if the parent can store calcium for making an egg shell, it can presumably store calcium to make it available to the embryo for skeletal formation.

The idea developed here that environmental variability provides strong selection, particularly among single-brooded species, for egg-

retention, egg-guarding, and viviparity seems to have considerable generality while being complementary to previous hypotheses. It provides an explanation for certain geographic and phylogenetic patterns in reproductive habits as well as an explanation for the greater frequency of viviparity in snakes than lizards and the relative rarity of tropical origin or invasion by viviparous species.

SUMMARY

The geographic and taxonomic distribution of viviparity is reviewed on a world-wide basis. The proportion of viviparous species in the squamate fauna is much higher at higher latitudes and elevations, but it is not true that viviparous species are most numerous in such areas. Instead they are most numerous at mid-latitudes and least so in the tropics or cold temperate regions. Viviparity is characteristically more frequent among snakes than among lizards. The widespread taxonomic distribution of viviparity suggests that it has evolved frequently in phylogeny and yet reports of the occurrence of both reproductive modes within a single species are exceedingly rare. Some support exists for the idea that the transition from oviparity to viviparity is more likely than the reverse.

The suggested correlations between the evolution of viviparity and arboreality, aquatic life and other life styles have been shown to lack generality. Incubation times and gestation times are not generally longer in temperate species than in tropical ones nor do we find evidence that viviparous species have shorter developmental times than oviparous ones, even in the same environments. Very short incubation periods of a few days to a few weeks are common in reptiles and indicate the widespread occurrence of intermediate stages between oviparity and viviparity. Egg-guarding, which is frequently associated with egg-retention, may be viewed in some sense as an alternate strategy to viviparity and one that may allow the parent the option of producing second clutches during the developmental period and of relief from the burden of carrying young. Egg-guarding may have arisen from a passive association between parent and eggs and may be most common in environments in which resources for the parent are minimal at the time of egg-laying.

The evolution of viviparity in our view occurs mostly in those environments in which breeding seasons are sufficiently short to restrict most reptiles to a single brood per year and in which conditions favorable for the development of the young are relatively variable during the reproductive period. In more predictable regions with long breeding seasons viviparous individuals may be at a large disadvantage to oviparous ones because of a restriction on fecundity. These considerations seem to explain the greater abundance of viviparous species in the temperate zones compared to the tropical

regions. They also explain the relative rarity of multiple-broodedness among temperate reptiles compared to tropical ones.

The absence of viviparity in turtles is suggested to be related to most species reproducing in a habitat different from that in which they live and to the assurance of a continued supply of resources for the adult which seems to permit multiple clutching, even in north temperate species. The absence of viviparity in crocodilians is correlated with their tropical distributions and with the predominance of nest-guarding among them.

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