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REPRODUCTIVE CYCLES IN TROPICAL REPTILES

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INTRODUCTION

Relatively little was known about reptilian reproduction up to the middle of the present century, but in the 1960s interest in the subject increased greatly. Many field and laboratory studies were made in the United States and other parts of the Temperate Zone. Studies of tropical reptiles lagged somewhat but in the 1970s such studies burgeoned. Excellent reproductive studies have now been made of reptiles of every major group and in almost every part of the tropics. The present paper represents a first attempt to synthesize the extensive literature on reproduction of tropical reptiles.

NATURE AND CAUSES OF REPRODUCTIVE CYCLES

Reproductive cycles involve regular, closely integrated changes in the anatomy, physiology, and behavior of a species, and are controlled by either intrinsic factors (internal rhythms) or extrinsic factors (temperature, moisture, food supply; Moll, 1979). The male and female cycles tend to be synchronized, but that of the male is generally somewhat accelerated in relation to the female's, so that in most populations males are ready to mate well before the females. Reptilian sperm cells are long-lived, and may remain viable in special receptacles in the females' oviducts for months or even years after mating (Goin, Goin and Zug, 1978). Hence, closely synchronized male and female cycles are not essential in all species for effective mating to occur.

In the male the reproductive cycle involves change in size and weight of the testes and intromittent organ, the associated glands, and the stage of development of the gametes, or their relative numbers. Also it may involve development of secondary sexual structures or colors, which are associated with aggressive display, fighting or courtship. In the female the chief morphological

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changes are in the ovaries and oviducts. Ovarian follicles grow through vitellogenesis and eventually are ovulated. The oviducts undergo change, with enlargement, thickening, and convoluting to receive the ova and add layers of albumen and shell to them, preparing them for oviposition in oviparous species. In viviparous species implantation of the egg in the oviduct occurs, and connection between embryonic and maternal tissue develops. Corpora albicantia and corpora lutea develop in the ovaries after follicles are released. In both sexes abdominal fat bodies may be present, and their growth or shrinkage reflect the stage in the reproductive cycle. They are largest when the gonads are small and inactive, and in some cases at least, they seem to function as a reserve store of nutrients which can be drawn upon to produce eggs or energy for fighting, courting or displaying.

In every stage of the reproductive cycle there is hormonally directed behavior, usually different in the sexes, and closely linked with changes in the gonads. In the male the cycle may involve establishing a breeding territory, displaying, fighting, courting and mating. In the female, behavior associated with the reproductive cycle follows a different sequence. One aspect of it is changing response to the male such as indifference, escape, hostility, tolerance, active search, and submissive posturing. Another sequence of activities is associated with nesting: search for a suitable site, perhaps with extensive migration; basking; depositing of eggs; covering and concealing nest; guarding, defending, or brooding of eggs. In general the female's cycle is more closely associated with reproductive success than the male's in its timing; therefore female cycles are the principal concern of this compilation.

Every species has evolved to its present state through millenia of natural selection, which has included, among other things, the timing of its reproduction. Thus, presumably, each is finely adjusted in its reproductive cycle to the timing of various events in the physical and biotic environments where it occurs. Wide ranging species vary geographically in their reproductive cycles, having adjusted to a variety of climates and biotic conditions either in specific adaptation to local conditions or in capacity to alter responses appropriately in adjustment to temporal and spatial environmental changes.

"Ultimate causes" in timing of the reproductive cycles are those that have brought about the adaptation of the species through natural selection. In contrast to these there are also "proximate causes" (Baker, 1938; Moll, 1979) which may provide the cues to which the species respond, but which are less fundamental than the ultimate causes. Both ultimate and proximate factors may be either endogenous (e.g. size, inherent rhythms) or exogenous (e.g. temperature, precipitation, photoperiod).

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Methods and Materials

This paper is a compilation based upon the findings of many herpetologists from field studies in various parts of the tropics, over a 70-year period. I have first-hand familiarity only with the mainland anoles and other Central American lizards, and my original data concerning these animals have already been published elsewhere. The findings of the many authors consulted have been arranged here in two subsections. First, selected groups are discussed to illustrate how, within each, animals basically similar in anatomy, physiology and life style have evolved diverse reproductive strategies. Second, several tropical regions are discussed, these selected on the basis of having had a variety of studies made on different types of reptiles. For each such region the reproductive cycle of at least one species is described in some detail, paraphrasing parts of the original author's account in an attempt to show how the animal's responses are attuned to various factors of the local climate and biota. In each instance, species sympatric with those discussed, but having different reproductive cycles, are compared.

This report was originally written in 1969, but of course has been extensively revised and updated to utilize the large amount of published literature that has become available. Publications appearing through early 1981 have been included. However, I have not attempted to summarize here all the literature pertaining to reproductive cycles of tropical reptiles, but have selected and presented in some detail accounts of certain species and certain areas that seem especially well suited to illustrate the important types of reproductive cycles and their diversity. Other species and areas that might have served equally well are allotted little space, or perhaps, inadvertently, omitted altogether in some instances.

Results

Reproductive Cycles in Selected Groups

Five important groups of reptiles, the sea turtles, anoles, lygosomine skinks, snakes, and crocodilians are discussed in the following account. Within each group there are basic patterns of reproductive cycles that are common to all, but with interspecific and intraspecific variants. The sea turtles are notable for the tremendous stress involved in the reproductive cycle. The female must make a migration, sometimes over great distances, to a traditional nesting beach, and must leave the security of the sea to deposit her eggs on land. The hatchlings in turn must find their way from the nest back to the ocean. More than any other reptiles, the sea turtles have evolved in the direction of producing eggs in great quantities (and relatively small size). Anoles are especially dependent on moisture for their reproduction but may also be influenced by temperature and photoperiod. In these small, slender scansorial lizards, clutch size has been reduced to the minimum of a single egg, with compensatory frequent oviposition. In the lygosomine skinks, mostly small, terrestrial-secretive lizards that are especially abundant in the paleotropics, reproductive cycles differ between regions and species, with extreme sensitivity to such environmental factors as moisture and temperature. In an aseasonal, rainforest environment there is generally year-round reproduction, but at changing levels, and the clutch is usually only two eggs. In climates subject to seasonal drought, breeding is limited to the wetter part of the year and clutches usually have three eggs or more. In snakes also, there is year-round breeding in some aseasonal equatorial regions, and a female may produce as many as six or seven clutches annually, but probably an output of two or three clutches is more typical. Many tropical snakes, including those that are live-bearers, produce a single brood per year. Crocodilians have a reproductive strategy that involves producing relatively large clutches of small eggs, with a single clutch annually, and with maternal care of the eggs and the young. There is a dichotomy in the timing and mode of nesting. Hole-nesting species oviposit in riparian sandbanks exposed by receding water early in the dry season, whereas mound-nesting species oviposit in elevated nests consisting of masses of decaying vegetation that the female has gathered, and nesting is timed to the rainy season.

Sea Turtles

Reproduction of the pantropical *Chelonia mydas* (Green Turtle) has been studied in detail in widely separated parts of the world (Bustard, 1972, 1979), notably in Sarawak on the island of Borneo, Surinam on the north coast of South America, and Tortuguero on the Caribbean Coast of Costa Rica in Central America (Carr and Ogren, 1960). The females of most populations do not produce annually, but typically have a 3-year cycle (two to four years). During her breeding season, the female may lay as many as 11 successive clutches (four is more typical), averaging about 110 eggs per clutch. These successive clutches are laid on the same beach and usually in the same general area. The 10- to 14-day interval between egg-laying is spent at sea in the vicinity of the "rookery," with concentrated courtship and mating activity. The years between nesting episodes are spent in feeding areas that may be remote from the rookeries, and the turtles must thus make long migrations (often 1000 miles or more) to or from the rookeries.

In Sarawak, in the Seychelles, and in the Gulf of Siam, egg-laying of *C. mydas* occurs year-round, and in these areas annual temperature fluctuations are minimal. However, in other known rookeries, egg-laying is seasonal and occurs through only part of the year depending on the extent of temperature change. Nesting of *C. mydas* takes place at night, but is influenced by the tide. Females emerge at high tide, and if this comes in early morning, before dawn, nesting may extend into daylight hours.

At Tortuguero on the Caribbean Coast of Costa Rica, green turtles lay most of their eggs in July, August and September, with the peaks in August—entirely within the rainy season. Females in their first breeding season lay an average of 2.7 clutches, with an average of 111.4 eggs per clutch. An average interval of 12.5 days intervenes between clutches. Old adults lay an average of 3.4 clutches with a mean of 116.8 eggs per clutch. For this population the usual interval between egg-laying seasons is three years, but some individuals are on a 2-year or 4-year breeding cycle. The age at sexual maturity is not definitely known, but is estimated to be in the range of 10-15 years (Bjorndal, 1980).

Chelonia mydas has been the subject of long and intensive study in East Malaysia (Sarawak, island of Borneo, Hendrickson, 1958). This population differs from others farther from the equator in that nesting occurs year-round. Typically an individual female returns to lay several successive clutches at an average interval of 10.5 days (contrasted with a 12.5 day interval for *C. mydas* at Tortuguero in the Caribbean) but then remains at sea for a three-year period.

The six other extant species of sea turtles are the cheloniids *Chelonia depressa, Caretta caretta, Lepidochelys kempi, L. olivacea,* and *Eretmochelys imbricata* and the single dermochelyid, *Dermochelys coriacea.* The latter is by far the largest sea turtle and also the most specialized. The seven species differ in economic importance, size, food habits and range, but all have in common certain fundamental morphological and ecological traits. In varying degrees all are giants compared with the average freshwater turtle, all require several or many years to reach maturity, and all are specialized for swimming, to the extent that locomotion out of the water is slow and difficult and occurs mainly when the female drags herself to the upper beach in order to lay her eggs. The front limbs are long flattened flippers while the hind limbs are small. All the sea turtles are tropical in distribution. While other marine reptiles, the acrochordid, hydrophiid and homalopsine snakes, and even the Mesozoic ichthyosaurs have evolved viviparity, the sea turtles, like other members of their order, have retained oviparity. Sea turtles produce large clutches; six of the seven species regularly lay more than 100 eggs at a time. Partly by mutual stimulation at the time of hatching, it is assured that members of the brood emerge from the nest almost simultaneously, and there is some safety in numbers as the large group of hatchlings make their way from the opened nest cavity on the upper beach down to the surf, running the gamut of a variety of predators, usually under cover of darkness. Some kinds of predators concentrate their attentions on the hatchling turtles, and individuals may travel long distances to be on hand at the time of emergence. The swamping effect on predators of the concentrated nesting by sea turtles is intensified when many females synchronize their nesting emergence at a given time and place. This is best exemplified by the "*arribada*" of *Lepidochelys kempi* on the coast of Veracruz.

The discoverer, H. H. Hildebrand, estimated that there were at one time 40,000 females present on a one-mile beach (Bustard, 1979). Although the hundreds of thousands of eggs produced in a single night by the *arribada* are too numerous to be destroyed by natural predators, the concentration of females leads to destruction of eggs and nests during the course of excavations. On a coral cay of Great Barrier Reef, Bustard (1972) found that for loggerheads (*Caretta caretta*) the probability of intraspecific nest destruction was 15%. However, green turtles nested in the same area, and the combined intra- and inter-specific nest destruction for loggerheads was near 40%.

Chelonia depressa produces only about 50 eggs per clutch, less than half the number typical of other sea turtles, and its eggs are correspondingly large. In this respect it contrasts with its near relative, *C. mydas*, which shares its nesting grounds on the Great Barrier Reef. Its large and powerful hatchlings are too bulky to be swallowed by the Silver Gull (*Larus novaehollandiae*) and too strong to be captured and held by the ghost crab (*Ocypoda ceratophthalma*), two of the main predators on green turtle hatchlings in the same region.

Despite large scale field studies in various parts of the world, sea turtle demography is still shrouded in mystery. The time required to grow from hatchling to maturity, survivorship and potential longevity, and habits of immature turtles are not well known for any species. Massive tagging operations on both hatchlings and adults have yielded records of outstanding interest, but have as yet failed to solve the major problems.

Anoles

The iguanid genus *Anolis* has more than 240 recognized species of which the majority live on the mainlands of Mexico, Central America and South America, but many others are endemics on the islands of the West Indies. In general the species are scansorial and favor warm and humid habitats. It is noteworthy that normally only one egg at a time is laid. The ovary and oviduct of the left side alternate with those of the right. Soon after an egg is laid, passing from the left oviduct, there is a new ovulation and the right oviduct in turn receives an egg which is fertilized, completes its growth, and receives a shell over a period of days. Meanwhile in the left ovary a follicle has made rapid growth, preparing for the next ovulation. As long as food and weather remain favorable, the cycle may continue, with ovipositions after regular intervals (Hamlett, 1952).

Anolis limifrons (Slender Anole) is a common species occurring from Mexico throughout most of Central America, chiefly in humid Caribbean lowlands, but extending into seasonally dry climates, and into mountains to medium altitudes. In the more humid part of its range, in rainforest climate, *A. limifrons* breeds throughout the year but with constantly changing level of reproduction tending to follow the amount of rainfall from month to month. For example at Finca La Selva in the Caribbean lowlands of Costa Rica, the ratio of ovigerous females to others was below average in January, February and March, was approximately twice as high in April, May and June, and gradually subsided from July through December. At Beverly, near the Caribbean Coast of Costa Rica, and at Turrialba, inland in a somewhat drier climate, the trend of reproduction roughly paralleled that at Finca La Selva; from mid-March to July there was steady increase in the rate of breeding, which attained its highest level in August, September and October, then subsided to a much lower level from December through April, the driest part of the year (Fitch, 1973b).

In the Panama Canal Zone, Sexton et al. (1971) studied reproduction of *A. limifrons* along a gradient from a relatively wet climate at the Caribbean end to a climate with severe seasonal drought at the Pacific end. They found that egg-laying is continuous throughout the year in the more humid climate of the Caribbean end, but ceases for several months, during the dry season, at the Pacific end less than 60 km distant. In confinement females from the Pacific study area could be stimulated to oviposit within a day by heavy sprinkling at any time in the dry season.

Water relations of eggs of *A. limifrons* and the sympatric *A. auratus* which occurs in more xeric grassland habitat, were studied by Andrews and Sexton (1981). In both species normal incubation of 44 days occurred in soils with 47%, 43%, 39% and 35% water content, but desiccation and death of the embryo resulted at 35% and 32%. Embryos of *A. auratus* survived longer in the unfavorably dry soils, and their eggshells had larger, more densely packed fibrils and a thicker matrix of calcium carbonate, rendering them more resistant. On the average, production of an egg every eight days in the rainy season (at La Selva, Costa Rica), and one every 19 days in the dry season (at Barro Colorado, Panama Canal Zone) has been found in *A. limifrons* (Andrews, 1979; Andrews and Rand, 1974). *A. limifrons* is typical of mainland rainforest species with prolonged breeding seasons in having the female larger than the male, and in having the male dewlap relatively small and unspectacular.

Anolis lineatopus of Jamaica, studied by Rand (1967) is representative of many Antillean species occurring on islands subject to marked seasonal change in amount of precipitation. The female *A. lineatopus* averages only 69 per cent of the male's linear dimensions and about one-third of his bulk. Males have large, colorful dewlaps which function in display, serving chiefly for territorial spacing. Adult males have ranges averaging perhaps four times as large (up to 20 m^2) as those of females and they tend to perch higher. Territories of adult individuals are relatively permanent from the rainy season with peak breeding activity to the dry season with a low level of reproduction. A male's territory may encompass several mutually exclusive female territories and these in turn may overlap territories of juveniles. The latter defend their areas only against conspecifics of similar size and flee from adults; cannibalism occurs occasionally. No two lizards of the same size can have widely overlapping ranges, but those of disparate sizes may overlap widely.

Data for 22 species of mainland anoles are presented in Table 1. Within this group there is a spectrum of reproductive cycles, from those that breed year-round in virtually aseasonal climates to those that have a short annual breeding season where drought prevails during the remainder of the year. It is evident that only those species living in a humid climate with no pronounced dry season reproduce throughout the year. Even in these the level of reproductive activity changes seasonally in response to the amount of rainfall. Each species whose range includes climatically different regions alters the timing and length of its breeding season accordingly.

Licht and Gorman (1970) and Ruibal et al. (1972) made comparative studies of the reproductive and fat cycles of several West Indian species on different islands representing a wide range of climates. Some of their data are summarized in Table 2.

Of the three Jamaican species both *A. grahami* and *A. sagrei* occur in more northern and seasonal climates, the former in Bermuda where it was introduced from Jamaica in 1906, the latter in southern Florida also introduced. In both instances reproduction comes to a halt for four to five months in the colder part of the year. The winter is cool and dry in southern Florida, 27°47′N, cool and relatively moist in Bermuda, 32°20′N. In both instances winter is sufficiently mild that no hibernation occurs. In Bermudan *A. grahami* of both sexes abdominal fat bodies were found to be more prominent than in the tropical anoles, and their size tended to be inversely proportional to the amount of reproductive activity.

The single-egg clutch of *Anolis* is closely linked with various other adaptations. Especially, it is correlated with the scansorial specialization characteristic of the great majority of anole species. Having only a single mature egg at a time, the female is minimally burdened, and her climbing ability, dependent on digital lamellae that permit clinging to a smooth surface, vertically or even upside down, is not seriously impaired. Despite the one-egg clutch, these small lizards are among the most prolific reptiles by virtue of their ability to maintain a high rate of production. Each ovary and oviduct functions in assembly-line fashion with vitellogenesis, ovulation, addition of nutrient materials and eggshells, and oviposition alternating on the left and right sides of the reproductive tract.

Lygosomine skinks

These are elongate, short-legged, smooth-scaled scincids that occur in great profusion in the Old World tropics. Most tend to be terrestrial-secretive; a few are arboreal. Most are small (less than 70 mm S-V) but some insular species are much larger, up to 288 mm S-V.

A pioneer study of reproductive cycles in these lizards was made by Baker (1947) at Espiritu Santo in the New Hebrides of Melanesia, 15°15′S. In this area of tropical rainforest, there are only 2° C difference in mean temperature between the warmest and coolest parts of the year, with a decrease in day length of one hour and 48 minutes from midsummer to midwinter. Rainfall exceeded 100 mm in each month. In the two species of skinks studied, *Emoia cyanura* and *E. werneri*, there was continuous reproduction throughout the year, but with constantly changing level, highest during the period from September to December. The increased egg production during this spring period corresponded with an increase in testis weight, and at the opposite time of year, fall and winter, egg production and testis weight declined to their lowest levels.

E. atrocostata was studied at Negros Island in the Philippines by Alcala and Brown (1967). Like the preceding species, it was found to have continuous breeding throughout the year, but no definite seasonal peaks were discernible. Incubation was found to last about 60 days, and growth to maturity required another nine or ten months. Immatures and first-year adults made up approxi-

TABLE 1. Seasonality of reproduction in some Mexican and Central American *Anolis*.

Species	Breeding season	Climate	Geographic area	Authority
attenuatus	year-round	cool and wet (driest Dec.-April)	Mountains, Costa Rica, 10°20′N	Fitch, Echelle, and Echelle (1976)
aquaticus	year-round	warm and wet (driest Dec.-April)	Mountains, S. Costa Rica, 8°30′N	" "
biscutiger	year-round	warm and wet (driest Dec.-April)	S. Costa Rica, Pacific, 9°30′N	" "
bourgaei	year-round	warm and wet	Gulf and Carib. versant, Central America, 15°-19°N	" "
*cupreus**	April-Sept.	warm; wet Apr.-Nov.; dry Dec.-Mar.	Pacific versant, Central America, 9°-15°N	Fitch (1973b)
cuprinus	July-Sept.	summer rains; long dry season	SE Guerrero, 16°25′N	Fitch, Echelle, and Echelle (1976)
*dollfusianus**	year-round?	warm and wet	SW Guatemala, 15°N	" "
dunni	July-Sept.?	summer rains, long dry season	S Guerrero and Michoacan, 18°N	" "
gadovii	July-Sept.	summer rains; long dry season	S Central Guerrero, 16°N	" "
*humilis**	year-round	warm and wet	Caribbean lowlands, Central America, 9°-11°N	Fitch (1973b)

*intermedius**	Apr.-Oct.	cool and moist; dry Dec.-Mar.	Mountains, Costa Rica, 10°N	Fitch (1973b)
isthmicus	July-Sept.	summer rains; long dry season	SE Oaxaca, 16°20′N	Fitch (1978)
*lemurinus**	year-round?	variable	Central America, 8°-15°N	Fitch (1973a)
*limifrons**	year-round	warm and wet	Caribbean lowlands, Central America, 9°-15°N	Fitch (1973a)
*lionotus**	year-round	warm and wet	Nicaragua, Costa Rica, Panama, 9°-12°N	Fitch (1973a)
megapholidotus	June-Sept.	summer rains	Mountains, Central Guerrero, 17°N	Fitch, Echelle, and Echelle (1976)
nebuloides	possibly year-round	warm and wet	Mountains, East-Central Oaxaca, 17°N	Fitch (1978)
nebulosus	June-August	summer rains; long dry season	Mexico; W. Coast, 17°-26°N	Jenssen (1970)
quercorum	June-Aug.?	cool and moist	Mountains, NW Oaxaca, 17°30′N	Fitch (1978)
subocularis	June-Oct.	summer rains; long dry season	S Guerrero, 17°N	Fitch, Echelle, and Echelle (1976)
taylori	July-Oct.	summer rains; long dry season	S Coast Guerrero, 17°N	Fitch, Echelle, and Echelle (1976)
tropidolepis	year-round	cool and wet	Mountains, Central Costa Rica, 10°N	Fitch (1973b)

* Species in which reproductive cycle is known to change in response to climatic change in different parts of the range.

TABLE 2. Seasonality of reproduction in some Antillean *Anolis*

Species	Breeding Season	Climate	Geographic Area	Authority
acutus	More than 50% ovigerous most months, relatively few Dec.-Mar.	Wet, 75-165mm per mo. May-Dec.; less than 50mm per mo. Feb.-Mar.	St. Croix 18°N	Ruibal et al. 1972
conspersus	Most reproductive Sept., Oct. Half or fewer reproductive Dec.-Jan. dry season.	Wet, with winter dry season.	Grand Cayman 18°20′N	Licht & Gorman, 1970
cybotes	Most ovigerous Mar. through Oct., fewer Apr., May, Nov., fewest Nov. through Jan.	Wet, often over 200 mm Apr., May, Oct., Nov., sometimes < 50 Dec.-Mar.	Hispaniola 18°30′N	Licht & Gorman, 1970
grahami	Nearly all ovigerous May-Oct. About 50% ovigerous Nov.-Apr.	Wet, with winter dry season.	Jamaica 18°N	Licht & Gorman, 1970
lineatopus	Most ovigerous May-Nov., few ovigerous in dry season.	Wet, with winter dry season.	Jamaica 18°N	Licht & Gorman, 1970
richardi	Virtually all reproductive.	Wet, variable; dry season Jan.-Mar.	St. Vincent 13°15′N	Licht & Gorman, 1970
sagrei	Nearly all ovigerous May-Oct.; < 50% ovigerous Dec.-Apr.	Wet, with winter dry season.	Jamaica 18°N	Licht & Gorman, 1970
trinitatis	About 80% ovigerous most months, 40% Jan.-Mar.	Wet, variable; dry season Jan.-Mar.	St. Vincent 13°15′N	Licht & Gorman, 1970

mately 70% of the population.

In northern Australia at 16° S, Wilhoft and Reiter (1965) studied a population of *Carlia fusca*, and found that the breeding season was limited to summer—October through February. By March no females were ovigerous and accessory sex structures in both males and females were undergoing regression. In *C. rhomboidalis*, also of northern Australia, Wilhoft (1963) found breeding throughout most of the year, with the following percentages of females gravid in the monthly samples of January through December: 15, 19, 15, (no Apr. sample), 20, 20, 0, 0, 9, 6, 12, 19.

Lygosomine skinks are prominent in the African fauna. Closely related sympatric kinds in the west African savanna differ markedly in their reproductive cycles, depending whether they are terrestrial or subterranean, and whether their habitat is open grassland, subject to seasonal burning, or the more stable habitat of gallery forest (see page 37). Those of the grassland tend to have more eggs per clutch but have a more restricted breeding season. Those of the forest tend to have few eggs per clutch but compensate with a relatively long breeding season.

From his own studies and from the literature Barbault (1975a) compiled a table of clutch sizes in 37 species of tropical and subtropical skinks. For 15 species considered characteristic of open habitats and having seasonal reproduction, clutches averaged 5.82 eggs (2.2 to 9.5) whereas in 22 species of humid forest habitats, and having continuous breeding, average was 2.57 eggs (1.9 to 6.0). At Lamto, Ivory Coast, the maximum annual production was found in the savanna species (average 30.4 eggs in *M. maculilabris*) despite the fact that year-round production occurs in the forest species.

Table 3 summarizes limited reproductive data for a large number of lygosomines. It shows that two is the usual clutch size for the group, with only one egg in some, but larger broods in some others are correlated with viviparity, with seasonal climates, and/or with exceptionally large body size.

Snakes

Reproductive cycles are less well known in tropical snakes than in other groups of reptiles. In Temperate Zone species, mating occurs in spring (and/or in autumn before retirement into hibernation). Often ovarian follicles are small at the time of mating, but they grow rapidly over periods of weeks, ovulation occurs in late spring or early summer, eggs are laid, usually before midsummer, and hatching (or birth of young) occurs in late summer or early autumn. Typically a female produces one brood each year. However, records are accumulating, mostly from snakes kept in zoos but

TABLE 3. Clutch and litter sizes in some tropical Lygosomine skinks

Genus and species	Ovip. or vivip.	Clutch or litter	Variable or constant	Adult size, SVL, mm*	Region of occurrence	Climate	Authority
Afroablepharus wahlbergi	O	1-6	var.	S	E Africa	seasonal	Greer, 1974
Carlia 30±sp.	O	2	con.	S	Austr. (N and E), New Guinea, etc.	humid	Greer, 1974
Cophoscincopus durus	O	2	con.	S	W Africa	seasonal, mainly humid	Greer, 1974
Cryptoblepharus boutoni	O	2	con.	S	Samoa	variable	Schwaner, 1980
Cryptoblepharus 36±sp.	O	1-2	con.	S	Africa, Australia, Oceania	variable	Greer, 1974
Emoia 40 sp.	O	2	con.	M-L	SE Asia, Polynesia, New Guinea	variable	Greer, 1974
Emoia nigra	O	$\bar{x} = 2.32$	var.	L	Samoa	variable	Schwaner, 1980
Emoia samoensis	O	$\bar{x} = 5.3$	var.	L	Samoa	variable	Schwaner, 1980
Eugongylus 3 sp.	O	up to 4	var.	L	Melanesia, etc.	variable	Greer, 1974
Geomyersia glabra	O	1	con.	S	Bougainville Island	humid	Greer, 1974

Leiolopisma 33 sp.	O-V	up to 9	var.	M-L	Austr., SW Pac. Is., Indian Ocean	variable	Greer, 1974
Lipinia leptosoma	O	1	con.	S	Palau Islands	humid	Greer, 1974
Lipinia vittigera	O	2-4	var.	S	SE Asia	variable	Greer, 1974
Lipinia 20 sp.	O-V	2	con.	S	Indo-Austr. Arch., Pacific Islands	variable	Greer, 1974
Mabuya quinquetaeniata	O	$\bar{x} = 4.8$	var.	M	Zambia	seasonal	Simbotwe, 1980
Mabuya striata	V	$\bar{x} = 4.2$	var.	M	Zambia	seasonal	Simbotwe, 1980
Menetia greyii	O	2	con.	S	Australia	variable	Greer, 1974
Morethia 6 sp.	O	up to 6	var.	S	Australia	variable	Greer, 1974
Panaspis 25 sp.	O	up to 5	var.	M	tropical Africa	variable	Greer, 1974
Prasinohaema 4 sp.	V	up to 9	var.	M	New Guinea	variable	Greer, 1974
Prasinohaema virens	O	2	con.	M-L	New Guinea, Solomons	variable	Greer, 1974
Sphenomorphus cherriei	O	$\bar{x} = 2.33$	var.	S	Costa Rica	humid	Fitch, 1973b

* S(small) = <65; M(medium) = 65-99; L(large) = 100-288.

also from some under natural conditions, to indicate that occasionally a female may produce a second clutch after a period of weeks, within the same season, and that also a female may skip one or more seasons between successive broods.

In tropical regions, especially those that tend to be aseasonal, with humid climates, there is opportunity for year-round breeding. However, most studies of tropical snakes have shown either that reproduction is limited to one time of year, or if there is an extended breeding season, it reaches an annual peak and declines to much lower levels at other times of year. Neill (1962) concluded from the seasonal incidence of gravid females and of hatchlings that the snakes of Belize (about 17° N) breed mainly in spring like their Temperate Zone relatives. He suggested that this spring breeding was a carry-over in a fauna mainly derived from more northern progenitors. Henderson and Hoevers (1977) rejected Neill's interpretation and provided evidence that Belizean snakes are relatively inactive during the dry season occupying the winter and early spring months, but become active and reproductive with the advent of the late spring rainy season.

Saint Girons and Pfeffer (1971) recognized six different reproductive patterns in Cambodian snakes. One of these patterns was "polyestrous" with aseasonal reproduction; but others were mostly "monoestrus" differing mainly in the time of year when reproduction occurred. Several field studies of tropical snakes have demonstrated extended breeding seasons, covering much of the year, or perhaps all of it. There is usually only scanty information, or none at all, to show how the performance of an individual female fits into such a regimen. An exceptional record is that of the female *Causus rhombeatus* at Accra, Ghana, which, in confinement, laid seven successive clutches at approximately monthly intervals (Woodward, 1933, see p. 37). Kopstein's (1938) studies also indicated a potentiality for at least six clutches annually for the Malayan *Xenochrophis vittata*.

Year-round breeding has been demonstrated or suspected in *Python sebae* at Lake Victoria Nyanza (Pitman, 1974), in various Amazonian snakes, including *Dipsas catesbyi, Imantodes cenchoa, Leimadophis reginae, Leptodeira annulata* and *Leptophis ahaetulla*; for Malaysian snakes, including at least *Homalopsis buccata* and *Xenochrophis vittata* (Kopstein, 1938), and for west Javan snakes including *Calamaria linnaei, Gongylosoma baliodeira, Rhabdophis subminiata* and *R. chrysarga* (De Haas, 1941). In contrast, a short and discrete annual breeding season has been found in many tropical snakes. These include all hydrophiines, (Bergman, 1943), most Indian snakes (Wall, 1921; Smith, 1943), and, in fact, tropical snakes wherever they occur in sharply seasonal climates, with one or more dry seasons in the annual cycle.

Zug, Hedges and Sunkel (1979) cautioned that ". . . we . . . must be aware of the potential diversity in reproductive cycles at a single site and the potential of a species for modifying its pattern at different locations." In the Temperate Zone of Southern Africa the snake fauna consists largely of species that range northward into the tropics. There are excellent works dealing with the temperate South African snake fauna (FitzSimons, 1962) and its more northern counterparts in subtropical Rhodesia (Broadley and Cock, 1975) and equatorial Uganda (Pitman, 1974). Many of the species in these three compilations are the same, revealing intraspecific latitudinal trends.

Obviously, reproductive cycles are affected by the method of reproduction, whether the species is oviparous or viviparous. Because of time required for gestation, typically around three months, viviparous species are rarely able to produce more than one brood per year, whereas oviparous species can produce two or more in favorable climates. Among 86 species of Ugandan snakes (listed by Pitman, 1974), 8.1% are oviparous, contrasted with the 10.5% in 76 Rhodesian species (listed by Broadley and Cock, 1975) and 9.1% in 105 South African species (listed by FitzSimons, 1962). These figures do not bear out the generally accepted idea that viviparity in reptiles is an adaptation to cool climate. In FitzSimons' (1962) volume on South African snakes every reference to the timing of reproduction indicates a spring breeding season. Broadley and Cock (1975) in their allusions to breeding of Rhodesian snakes, also indicated seasonal limitation, whereas Pitman's (1974) data indicated much longer breeding seasons in Uganda, but records were too meager to demonstrate whether any species maintained its reproduction throughout the year.

Species having a long breeding season in a tropical portion of the range could routinely produce more than one annual brood there, and might therefore tend to produce smaller broods than they would in a seasonal climate limiting them to a single annual brood. Eight such species are listed in Table 4. In the table, numbers in parentheses are taken from the authors' statements and the "estimated number" is averaged from them. In a second group of species (Table 5) the trend seems to be the opposite, that is from a larger number of eggs per clutch in tropical Uganda to fewer in temperate South Africa. For the entire assemblage of species shared by the three African areas the results are inconclusive in that more than half show no discernible trends and the remainder are about equally divided between those that increase brood size from south to north and those that do the opposite. In body size a clearer trend was revealed by the snake species occurring through the three areas. For 40 species there was an average gain of 7.05% from South Africa to Rhodesia, and for 20 of these that extended north into

TABLE 4. Snake species increasing brood size from African Tropics to Temperate Zone

Species	Vivip. or ovip.	Estimated number of young in brood South Africa	Rhodesia	Uganda
Aparallactus capensis	O	3(2-4)	2.5(2 or 3)	....
Bitis atropos	V	11.5(8-15)	7(about 7)	....
Bitis caudalis	V	15(12-19)	12(4-19)	....
Hemirhagerrhis nototaenia	O	....	6(4-8)	3(2-4) Tanganyika
Lycophidion capense	O	7(6-8)	6(3-9)	5.5(4-7)
Philothamnus irregularis	O	9(6-8 up to 16)	9(6-12)	6(4-8)
Philothamnus semivariegatus	O	9(6-12)	9(6-12)	(4)3-5
Pseudaspis cana	V	40(30-50)	20(about 20)	....

Uganda there was a 10.3% further increase. These trends are revealed from the maximum measurements (usually given for each sex separately) by FitzSimons (1962), Broadley and Cock (1975), and Pitman (1974). Larger females tend to be more prolific than smaller ones of the same species, hence the trend toward larger litters in the tropics for some is partly explained.

Crocodilians

Distribution is primarily pantropical in the crocodilians. However, there are species in the Temperate Zones in the southeastern United States, China and northern Argentina. The 21 living species are large or giant-sized reptiles, remarkable for the large amount of parental investment in reproduction, nest building, guarding of the clutch, releasing the young from the eggshell and nest in response to their calls, carrying them to safety of the water, and protecting them for periods of weeks or months. While most of these functions are performed by the female parent, the male may participate in some of them. All species are oviparous; the clutch is large, there is a single annual clutch, and the size differential between adult and hatchling is extreme. The mating system is polygynous, with dominant males defending territories inhabited by several or many females in those species studied under natural conditions.

Crocodylus niloticus (Nile Crocodile) has been studied in various parts of Africa. Widely different timing of breeding seasons is indicated in Table 6. However, in each instance the same set of environmental factors controls the timing. Fluctuation in water level is the critical factor. Laying occurs during the dry season, after the water level has been receding for several weeks. Incubation is in progress during the time of lowest water level, and hatching occurs after the onset of the rainy season, when water levels are rising—some 12 to 14 weeks later. In Sri Lanka, *Croco-*

TABLE 5. Snake species decreasing brood size from African Tropics to Temperate Zone

Species	Vivip. or ovip.	South Africa		Rhodesia		Uganda	
		Brood	♀ S-V	Brood	♀ S-V	Brood	♀ S-V
Causus rhombeatus	O	19(12-26)	684	20(about 20)	680	27(25-29)	640
Duberria lutrix	V	6(usually 6)	333	8(7-9)	345	9(6-12)	384
Naja haje	O	14(8-20)	----	22.5(20-25)	1946	----	----
Naja melanoleuca	O	15(about 15)	1271	21.5(17-26)	1550	----	2591
Prosymna sundevallii	O	3.5(3-4)	362	5(about 5)	325	----	----
Psammophylax tritaeniatus	O	8(6-10)	680	11.5(5-18)	660	----	----
Telescopus semiannulatus	O	8(6-10)	811	13(6-20)	865	----	----

TABLE 6. Breeding seasons of *Crocodylus niloticus*

Region	Time of Breeding	Authority
Upper Victoria Nile and Lake Kioga	Last 3 weeks of December	Cott, 1961
Victoria Nile below Murchison, and Lake Albert	Late Dec., first week of Jan.	" "
Bangweulu Swamp	Last week of Aug.; first half of Sept.	" "
Kafue, Luangwa and upper Zambesi rivers	First half of Sept.	" "
Kalungwishi River, Mweru Wa Ntipa	First half of Sept.	" "
Central island in Lake Rudolf	Late Dec. (laying)	Modha, 1967
Ndumu Game Reserve, Zululand	5 Nov. to 26 Dec.	Pooley, 1969

dylus porosus has been found to have a similar schedule, with nesting occurring in the hottest and driest part of the year, in July and August, and with hatching in the rainy season. However, in Arnhem Land, northern Australia, Webb et al. (1977) found nesting activity of *C. porosus* to be associated with the rainy season. Prior to their nesting, females move upstream from the rivers' lower reaches, into areas of lower salinities, or shift away from the rivers into freshwater swamps.

In their nesting strategies, including type of site utilized and timing of egg-laying in wet or dry season, crocodilians display a marked dichotomy, well illustrated by Webb's (1980) comparison of sympatric *Crocodylus johnstoni* and *C. porosus* in the coastal area of northern Australia. Like several other species, *C. johnstoni* excavates burrows in riparian sandbanks left by receding water during the dry season. Hatching occurs at the beginning of the rainy season. *Crocodylus porosus*, representative of another group of species, nests at the opposite time of year, in the wet season. Its nest is a mound of decaying vegetation, scraped together by the female. Its nesting season is relatively prolonged as compared with that of *C. johnstoni*, and hatching occurs from late in the rainy season to the middle of the dry season. Webb determined that in the hole-nesting, *C. johnstoni*, egg losses to predation were heavy (64% of nests) whereas flooding was a minor source of loss (2%). On the contrary, *C. porosus*, nesting in the wet season, lost up to 90% of its nests to flooding, but predation was relatively trivial. Mound-nesting species sometimes build their nests on floating vegetation in lakes or swamps. Staton (1980) noted that in the vicinity of San Fernando de Apure on the Venezuelan llanos in the 1976 season with unusually high precipitation, *Caiman crocodilus* often nested on floating mats of vegetation and near human dwellings, and that destruction of nests by humans was unusually high. In central Bolivia, Lovisek (1980) noted that 36 of 37 *C. crocodilus* nests were on floating mats of vegetation, and that 27% of all nests were destroyed by flooding, whereas predation was slight.

Table 7 compares the reproductive cycles of 10 crocodilian species.

Regional Trends

1. *Southern Central America*

Several intensive studies of reproductive cycles have been made in Costa Rica and Panama. Although the area involved is relatively small, this is a region of varied climatic regimes and diverse habitats with an extremely rich herpetofauna. Throughout Costa Rica and western Panama high mountain ranges separate lowlands of the Caribbean and Pacific versants. Even in the Canal Zone where high mountains are lacking, there is a climatic gradient from the humid Caribbean Coast to the seasonally dry Pacific Coast.

Two species chosen to illustrate the diversity of reproductive cycles are to some degree representative of the two main climatic types. *Pseudemys scripta,* a freshwater turtle of the Caribbean lowlands, and *Ctenosaura similis,* a large lizard characteristic of the Pacific side, both lay their eggs in the drier part of the year, and in this respect differ from most other Central American reptiles. However, they differ from each other in that *P. scripta* produces several successive clutches, *C. similis* only one.

Pseudemys scripta ("*Jicotea,*" a neotropical slider), an omnivorous, aquatic emydid, was studied by Moll and Legler (1971) at Juan Mina, Panama Canal Zone, 9°10′N. There is a pronounced dry season from mid-December through mid-April (monthly precipitation about 5 cm or less) and high rainfall at other times (20 to 50 cm per month) with the maximum in November. Reproduction is seasonal. Ovarian follicles begin to enlarge in the latter half of the rainy season, late August or September, and there is continuous development until late May. As one clutch of follicles matures and is ovulated, those of the next smaller class begin a period of rapid growth. Ovarian weights reach their maximum from January through March, the laying season, and testes also attain their maximum size then. At the height of the reproductive season a female ready to lay will have also a second clutch of full-sized follicles ready to be ovulated. The number of clutches produced (up to five or six) is directly proportional to the size of the female. Large and old females have a longer reproductive season than do smaller and younger ones; they may begin laying in January and continue into May. Nesting is limited to the dry season. Moll and Legler (1971) noted migration up to 3500 m for egg-laying. Clutches averaged

TABLE 7. Reproductive cycles of crocodilians

Species	Type of nest	Nesting season	Time of mating	Time of egg-laying	Time of hatching	Place of study	Authority
Alligator mississippiensis	Mound	Wet	Apr., May, June	Late June	Aug.	Louisiana	McIlhenney, 1935 Joanen & McNease, 1980
Caiman crocodilus	Mound	Wet	--------	Sept. (mid-Aug.-late Oct.)	Late Dec.-early Jan.	Venezuela, llanos	Staton & Dixon, 1977
Caiman latirostris	Mound	Wet	--------	Nov.-Dec.	--------	Central Bolivia	Lovisek, 1980
	Mound	Wet	Dec., Jan.	Jan.-Feb.	Mar., Apr.	N Argentina	Marc Nadeau pers. comm.
Crocodylus acutus	Hole	Dry	Jan., early Feb.	Mid-Feb.-early Apr.	Mid-May-early July	Dominican Republic	Inchaustegui et al., 1980
Crocodylus johnsoni	Hole	Dry	--------	Aug.	--------	N Australia	Webb, 1980
Crocodylus novaeguinae	Mound	Wet	Oct.-Dec.	Mainly Nov.-Dec.	--------	Port Moresby, New Guinea	Lang, 1980
Crocodylus palustris	Hole	Dry	Dec.-Jan.	Feb.-Apr.	Apr.-June	S India	Whitaker et al., 1980(1)
Crocodylus porosus	Mound	Wet	Oct.-Dec.	Mainly Nov.-Dec.	--------	Port Moresby, New Guinea	Lang, 1980
Gavialis gangeticus	Hole	Dry	--------	Mar.-Apr.	--------	India	Whitaker et al., 1980(2)
Osteolaemus tetraspis	Mound	Wet	Mar.-Apr.	May-June	--------	Ft. Worth, Tex. (from W Africa)	Tryon, 1980

17.4 (9-25) eggs. Incubation averaged 81 days in natural nests. Hatchlings often did not emerge promptly from the nest, but awaited heavy rain. Even after emergence they did not immediately make their way to the water, but led a terrestrial-secretive existence, often for two months or more. Males attain sexual maturity in two to four years (plastral lengths 125-135 mm) whereas females require five to seven years (240-260 mm). Growth is cyclic, and although there is some growth every month, increments are maximal during the dry season and are directly related to the amount of sunshine.

Pseudemys scripta is a polytypic species that occurs in a wide variety of climates and habitats, in the Temperate Zone as well as in the tropics. Compared with the Panamanian turtles studied by Moll and Legler (1971), those studied at various localities in the eastern United States are much smaller (ca 70% linear dimension), breed later (ovulation beginning in April rather than December), and for only three instead of six months, with eggs smaller, fewer per clutch (7-9 rather than 17) and in fewer clutches per season (1-3, instead of 1-6).

In contrast to the dry season nesting of *P. scripta*, is that of the marine green turtle, *Chelonia mydas*, which at Tortuguero nests entirely within the rainy season, and peaks in September. On the Pacific Coast at Ostional, some 250 km west of Tortuguero, another kind of sea turtle, *Lepidochelys olivacea* (Pacific Ridley) nests, also in the wetter part of the year. The west coast climate is relatively dry. The arribadas of *L. olivacea* occur in late September or in October, the time of year when precipitation is most concentrated (Zahl, 1974).

Ctenosaura similis (Ctenosaur) is a large iguanine lizard of Central America and southern Mexico, mainly in seasonally dry areas of the Pacific versant. There is a single annual breeding season and females produce but one clutch annually. During the rainy season, from about late April through November, when food is abundant, the abdominal fat bodies gradually grow to about six per cent of the female's total weight. Vitellogenesis occurs in late December, January and February. Ovulation reaches a peak in mid-February, and the peak of egg-laying is approximately five weeks later, in late March. During late stages of follicular growth, the abdominal fat bodies dwindle rapidly and by the time of ovulation they are inconspicuous, making up much less than one per cent of the female's total weight. Eggs averaged 43.4 (12 to 88) in a sample of 69 clutches (mean 22 eggs in probable two-year-olds, 70 eggs in probable 8-year-olds; Fitch and Henderson, 1978).

In the areas where *C. similis* reaches maximum abundance, the dry season lasts for about five months, December through most of April, with little or no rain falling during that time, and with habitats xeric in aspect. Eggs are deposited in burrows. The female does not need to search outside her usual area of activity to find a nest site, and no special stress is involved in nesting. There is a tendency for communal nesting. Several females may have nests in the same burrow system, but in separate chambers interconnected by a network of subterranean passages (Wiewandt, in press, citing a manuscript by Hackforth-Jones and Harker). Gravid females may occasionally eat the eggs of others. Most hatching occurs in June. Incubation lasts a little less than three months and begins late in the dry season, but at least the latter two-thirds takes place within the rainy season. By the time the hatchlings appear, the rigors of the dry season are past. New green foliage has appeared and insects are abundant, providing, respectively, shelter and food.

Iguana iguana (Green Iguana) is like *Ctenosaura* in some aspects of its ecology and reproduction, but is different in many details. This giant arboreal herbivorous iguanid ranges from the northern limits of the tropics on both coasts of Mexico, southward through most of Central America and much of South America. There is a single annual clutch of eggs ($\bar{x} = 30.5$), and primiparous females produce only about one-third as many eggs (13.4) as old adults (44.5). Mating behavior has been studied intensively by Dugan (in press) at Flamenco Island at the Pacific entrance to the Panama Canal. Adult males may be classed as large, medium, or small. These categories are largely age-dependent and have important bearing on behavior and mating success. Ordinarily only large males maintain breeding territories, and they accomplish more than 90 per cent of the mating. Their testes have enlarged by early November. In that month large males are active in securing and defending a territory which consists of a large, conspicuous tree with display perches. Display, courtship and territorial patrol alternate with rest periods but there is little or no feeding. Individual females are courted for about a month before becoming receptive, and receptivity lasts for at least 15 days, the female copulating from one to five times, usually with the same male. Copulation occurs mainly in December. Medium males are not able to maintain territories and are excluded from the territories of large males, but they tend to loiter near edges of territories and attempt to intercept females. Small males do not hold territories, but being much like females in appearance, they are often able to remain within the territory of a large male for fairly long periods, avoiding the dominant male but subject to attack and pursuit. A small male will at every opportunity attempt copulation with resident females but such attempts rarely succeed because females resist vigorously and territorial males are alert to attack such interlopers and protect the females. A breakdown of territories occurs in late January coinciding with ovulation and the termination of receptivity in females, and reduction in size of male testes. Egg-laying occurs in February and March, and females may migrate as much as 3 km to find nest sites in suitably open, sunny habitat, typically a sandbar left exposed by falling water level. The females are often gregarious in their nesting; several or many congregate with frequent threatening and scuffling resulting from competition over preferred sites or burrows. Eggs require 10 weeks of incubation. Hatchlings, having dug their way to the surface, are slow and cautious in emerging (Burghardt, Greene and Rand, 1977). They remain under cover while scrutinizing their surroundings, and in the initial dash from the burrow entrance several may move together or in rapid succession. Emigrating from the area of the nest, they move as a loose group maintaining visual contact, each tending to follow the path of one that has preceded it, in a series of dashes, with intervening pauses in sheltered spots. Hatchling iguanas are about three times the bulk of hatchling ctenosaurs. However, primiparous females produce eggs less than three-fourths the size of those produced by large adults.

In 16 lizard species studied in Costa Rica (9°-11°N), I found five types of population structure resulting from different types of reproductive cycles (Fitch, 1973a, see Table 8). The species assigned to Type I, II and III all produce several or many clutches during an annual cycle. On the contrary the two live-bearers of Type IV and the two giant iguanines of Type V are all single-brooded. In some instances young that appear early in the breeding season (Types I, II and III) attain maturity and contribute their own clutches before the end of the breeding season.

Several of the species studied at more than one locality were found to alter their reproductive patterns markedly in response to local climatic conditions. *Gonatodes albogularis* is a continuous breeder (Type I) in the humid climate of Limón on the Caribbean Coast, but at Boca de Barranca on the Pacific, breeding stops for several months during the dry season. At Tortuguero, Hirth (1963) found somewhat different seasonal trends in *Ameiva quadrilineata* than I found at Quepos on the opposite Coast (Fitch, 1973b), and at Pandora, with even higher rainfall, Smith (1968) concluded that there was no seasonal variation in reproduction (Type I).

Near its lower altitudinal limits 1200-1800 m, *Sceloporus malachiticus* brings forth its young in December and early January. These young are approaching adult size by the following June, maturing in time for the August-September breeding season in the middle of the rainy season. Neonates appear at the beginning of the dry season and much of their growth occurs within the dry season. At high altitudes this fixed seasonal schedule seems to break down. The low prevailing temperature, with frequent cloud or mist cover prevents maintenance of preferred body temperature and delays attainment of sexual maturity within the first year. Further-

TABLE 8. Reproductive cycles and population structure in Costa Rican lizards

Type of Cycle	Species	Climate	Area	Breeding Season	Population structure
I	*Anolis humilis*, *A. tropidolepis*, *Gonatodes albogularis* (Caribbean)	Wet, little seasonal change	Caribbean rainforest; montane cloud forest	Year-round with little variation	All ages constantly present with little seasonal change.
II	*Anolis limifrons*, *Basiliscus vittatus*, *Ameiva quadrilineata*, *Sphenomorphus cherriei*	Wet with some seasonal variation	Caribbean lowlands	Year-round with changing levels	All ages constantly present with seasonal change in ratios.
III	*Ameiva undulata*, *Anolis cupreus*, *A. intermedius*, *Gonatodes albogularis* (Pacific), *Cnemidophorus deppei*, *Sceloporus variabilis*	Variable; dry season Dec.-Apr.	Meseta Central, Pacific lowlands	Rainy season, mostly May-Nov.	Only adults and subadults at start of breeding season; immatures, hatchling to adult size, also present at end of breeding season.
IV	*Gerrhonotus monticolus* *Sceloporus malachiticus*	Humid; drier Dec.-Apr.	Meseta Central and mountains	Early rainy season; viviparous	Variable according to altitude and season; *S. m.* matures in first year, *G. m.* probably requires two years or more.
V	*Ctenosaura similis* *Iguana iguana*	Variable; dry season Dec.-Apr.	Pacific lowlands *C. s.* Pacific and Caribbean lowlands *I. i.*	Early dry season	Discrete annual age classes; first- and second-year young distinguishable from adults.

more, the dry season is less well defined than at lower altitudes, and births seem to occur at all times of year.

Relatively little is known about the reproductive cycles of Central American snakes. Zug, Hedges, and Sunkel (1979) studied reproduction in 88 female *Coniophanes fissidens,* but results were somewhat inconclusive because of small samples and varied provenance (southern Mexico to Ecuador). There were reproductive females in samples from January through August, but none from September through December (no specimens available for September and only one each for the other three months). In July and August when the largest samples were available, only 6 of 23 and 4 of 29, respectively, were reproductive, but the ratios were higher from March to May. Obviously the breeding season is lengthy, overlapping both dry and wet seasons, so it may be suspected that there is some breeding year-round.

2. *South American Rain Forest*

This includes a vast lowland area in the basins of the Amazon, Orinoco and other rivers, characterized by high precipitation through most of the year. Many of the reptile species have remarkably extensive ranges. The rich herpetofauna includes many kinds of turtles, lizards, snakes and crocodilians, with a diversity of reproductive cycles.

Podocnemis expansa ("Arrau"), a giant pleurodiran turtle, is an important member of this herpetofauna. Its reproductive cycle has been described by Roze (1964). As a primary consumer it attains high population density and biomass. Adult females average about 60 cm in carapace length (20-25 kg) and males are about three-fourths of female length. Nutritious parts of plants including flowers, fruits and roots are eaten as the turtles wander through the flooded forests in the wetter part of the year. In January in the Orinoco region Arraus cease feeding and begin a migration downstream along tributaries to the main river channel then either downstream or upstream to traditional nesting areas, sandbanks of large islands. When migration begins, the nesting areas still may be as much as nine meters underwater but water level is already falling. Males arrive first, females appear on the islands where nesting will occur in late January, and begin basking on the sand at the edge of the water. After several days numbers have increased from an initial few to hundreds or thousands, so closely packed that newcomers have difficulty finding spots to bask. Several hours each day over a period of weeks are spent basking while the eggs are developing, and the turtles maintain much higher body temperatures than at other times. Between 11 January and 25 February, eggs complete their uterine development and are ready for laying. The females emerge and wander slowly over the sandbars in groups under cover of darkness testing the sand for suitable nest sites. The sites finally chosen are on the highest parts of the sandbanks. At first the female digs with all four feet to scoop out a depression .6 m deep in the dry sand of the surface layers, then she excavates the actual nest cavity with her hind foot. Eggs average about 84, but are fewer in the smaller and younger females, and the recorded maximum is 150. The female places the eggs with her tail, arranges them in a single layer, covers the nest and fills in the depression above it, smoothing over an area of perhaps 3.5 by 1.5 m. She leaves a small depression at the end of the smoothed area, well removed from the actual nest, which may serve to mislead predators. The eggs require at least 45 days of incubation, and the hatchlings require at least two or three days to dig to the surface. Emergence is at night or in early morning. Upon emerging the young scuttle rapidly downward toward the water, but are beset by many enemies that take a heavy toll. Vultures *(Coragyps atratus)*, Caracaras *(Caracara plancus)*, Jabiru Storks *(Jabiru mycteria)*, and Ibises *(Mycteria americana)* congregate in anticipation of the abundant food supply. Crocodiles, caimans and several kinds of large fish take further toll on those that reach the water. In some years heavy rains are much more destructive than all these predators combined as they cause the river level to rise and flood the nesting areas before the eggs hatch or before the hatchlings have dug to the surface. Millions of casualties in a single season may result from such natural catastrophes. The Arrau is admirably adapted to withstand the toll of both predators and floods, but its numbers have dwindled rapidly under heavy exploitation of its eggs by humans.

The Arrau is widely distributed in the South American lowlands, and its seasonal schedule varies (Vanzolini, 1977). In Brazil the laying season is December for the Río Negro, October for the Trombetas and Tapajós and September-October for the Purus. Several other species of *Podocnemis* occur in the same region, with large scale sympatry. All are much smaller than *P. expansa:* the smallest, *P. vogli*, is only a little more than one per cent of the bulk of *expansa* (less than .5 kg vs. 45 kgs) and one-fifth its linear dimensions. Among the important ecological differences are seasonal schedules. *Podocnemis dumeriliana* and *P. erythrocephala* lay their eggs in August-September at the Río Negro (*expansa* and *unifilis* in December), and *unifilis* and *sextuberculata* lay in June-July at Río Purus (*expansa* in September-October). However, at the Río Trombetas *unifilis* lays only a little earlier than *expansa*, and at the Río Negro at about the same time. *Podocnemis vogli* and *P. unifilis* may wander far from the water to lay and will accept a variety of substrates other than the sand required by *P. expansa*. These two have calcareous eggshells. *Podocnemis dumeriliana* nests in leaf litter and mud. All the smaller species have clutches of relatively few eggs compared with *P. expansa.* There is evidence of *P. vogli* and *P. unifilis* laying twice in the same season.

At Santa Cecilia on the Río Aguarico, an Amazon tributary in Ecuador near the east base of the Andes, Duellman (1978) found more than a dozen species of small lizards to be year-round breeders. These included all the species of *Anolis* present in that area (*A. chrysolepis, A. fuscoauratus, A. ortonii, A. punctatus, A. trachyderma, A. tranversalis*) and also included *Gonatodes concinnatus, Pseudogonatodes guianensis, Plica umbra, Kentropyx pelviceps, Leposoma percarinata, Neusticurus ecpleopus* and *Prionodactylus argulus.* In the same region he found noncontinuous breeders included *Thecadactylus rapicaudus, Enyalioides cofanorum, E. laticeps, Alopoglossus atriventris, A. copei, Ameiva ameiva* and *Mabuya mabouya.* Thus iguanids, geckonids and teiids had representatives of both groups, and in some instances these were closely related. Duellman noted that all the continuous breeders are small (usually less than 100 mm S-V); all are oviparous and most produce only one or two eggs at a time.

In the vicinity of Iquitos in Amazonian Peru some 600 km southeast of Santa Cecilia, Dixon and Soini (1975) obtained reproductive data on numerous species and found evidence of year-round breeding in *Gonatodes humeralis, Pseudogonatodes guianensis, Anolis bombiceps, A. fuscoauratus, A. punctatus, A. trachyderma, Plica umbra, Alopoglossus atriventris, Neusticurus ecpleopus* and *Prionodactylus argulus.*

In another part of the South American rainforest, in Surinam some 2500 km east and somewhat north of the Santa Cecilia and Iquitos region, Hoogmoed (1973) studied a similar biotic community with some of the same lizard species. He found evidence of year-round breeding in *Gonatodes humeralis, Anolis auratus, A. chrysolepis, A. fuscoauratus, Polychrus marmoratus* and *Kentropyx calcaratus.* In several other kinds he found seasonal breeding; *Mabuya mabouya* bears young from late August to late September; *Ameiva ameiva* is ovigerous in May and in September-October-November, seemingly with two distinct breeding seasons; *Kentropyx striatus* is ovigerous in October, November, and January, in the "long dry" season. *Arthrosaura kockii* starts its breeding early in the wet season, in August, and continues at least until February. *Leposoma guianensis* females have been found gravid in March and hatchlings have been found in February, May, August, and September. Breeding seems to occur through most of the year, but perhaps not in the "long dry" season. *Plica umbra* has been found gravid through much of the year, but perhaps does not breed during the June-July-August period.

Two closely related tropidurine iguanids, the saxicolous *Platynotus semitaeniatus* and the more generalized *Tropidurus torquatus,* were compared in their reproduction where they occur sympatrically in semi-arid thorn scrub forest, near Exu, 7° 25′ S, Pernambuco, eastern Brazil (Vitt, 1981). Clutch ranged from 3 to 14 ($\bar{x} = 7.3$) in *T. torquatus* but was almost invariably 2 eggs in *P. semitaeniatus.* Both the lizards themselves and their eggs are about the same size in these species, but eggs of *P. semitaeniatus* are elongate, deviating from the usual iguanid shape, and females produce as many as four clutches per year. Vitt interpreted the reproductive traits of *Platynotus* as aspects of saxicolous adaptation; with a 2-egg clutch and elongate eggs, even gravid females are still able to squeeze into narrow crevices in rocks, where they are relatively secure from predation.

Also in the Exu region, Vitt and Lacher (1981) studied ecology and reproduction of the large anoline *Polychrus acutirostris.* Females are twice the bulk of their male counterparts, and produce one annual clutch with a mean of 17.9 eggs, but with old adults producing clutches nearly twice as large (22.0) as those of first-year individuals (11.6). Oviposition occurs at the beginning of the wet season, with hatching at the end of the wet season or early in the dry season. Young of both sexes mature in time for the next breeding season.

Reproductive cycles of South American snakes are less well known than those of lizards because local samples are generally much smaller. Thousands of snakes were assembled from the vicinity of Iquitos, Peru, in the Bassler collection of the American Museum of Natural History. Year-round reproduction is suggested in those species for which sufficient data were available, especially *Leimadophis reginae, L. taeniurus, Leptodeira annulata, Leptophis ahaetulla,* and *Bothrops atrox* (Oliver, 1947; Fitch, 1970) on the basis of finding of gravid females and/or hatchlings well distributed through the year. Allegedly, collecting effort was on approximately the same level for several years in the assembling of the Bassler collection. However, for some months no adult females were collected, and for other months there were only one or two, so that the absence of gravid individuals did not necessarily indicate nonbreeding in the species. Dixon and Soini (1977) presented further data on the reproduction of 43 species of Iquitos snakes, supplementing the earlier records (Oliver, 1947; Fitch, 1970). For *Leimadophis reginae, Leptodeira annulata, Leptophis ahaetulla* and *Bothrops atrox,* especially, strong evidence of year-round reproduction is provided by the combined sets of data. These are the species for which most data are available. On the other hand, there is as yet no evidence that any of the Iquitos snakes are limited to certain times of year in their reproduction.

Dipsas catesbyi and *Imantodes cenchoa* are among the best known of South American snakes in their reproduction, through the work of Zug, Hedges and Sunkel (1979). Gravid females of *D. catesbyi* are known from February, March, April, June, September and December. Although these records are widely scattered geographically (Ecuador in April and June; Peru in February, March, April, September, December), they suggest year-round reproduction. In *Imantodes cenchoa* hatchlings are known from every month except February, June and October, suggesting year-round breeding, although, again the records are widely scattered geographically.

In the semi-arid area of northeastern Brazil where rain forest gives way to "caatingas" with xeric scrub forest, reproduction is more seasonal. In a study of the reptiles of the caatingas, Vanzolini, Ramos-Costa and Vitt (1980) found the majority of species limited to a short annual breeding season and a single clutch or litter. Species typical of this pattern are the lizards *Iguana iguana, Polychrus acutirostris, Tropidurus torquatus, Tupinambis teguexin,* and the snakes *Waglerophis merremi* and *Crotalus durissus.* Among the few species deviating from this pattern were several geckos, the lizards *Platynotus semitaeniatus, Ameiva ameiva* and *Cnemidophorus ocellifer* (several clutches per year), *Mabuya heathi* (2 litters), and the snakes *Dromicus poecilogyrus* (2 clutches), and *Liophis mossoroensis* (no distinct breeding season).

3. *Galapagos Archipelago*

This group of volcanic islands straddling the equator in the Pacific Ocean nearly 1000 km off the west coast of South America is famous for the evolutionary studies of Charles Darwin and many later scientists. There are some 19 named islands (up to 130 km in longest diameter), 42 substantial islets and numerous smaller islets and rocks distributed over an area about 370 x 214 km. The climate is arid and the fauna is meager. The climate is cooled by the Humboldt Current flowing north along the west coast of South America. This current envelops the islands from June to December, the *garúa* or dry season, when air temperature seldom exceeds 25°C and persistent damp, heavy mist is usually present, with often no more than an hour or two of sunshine daily. From December to May a warm northern current displaces the Humboldt, bringing higher average air temperatures and heavy intermittent rains (average from 25 to 150 mm per month) alternating with dry, sunny weather. The islands differ greatly in size and in degree of isolation from each other (by actual distance and also by prevailing ocean currents) and each has a unique fauna with a high incidence of endemism.

Geochelone elephantopus (Galapagos Giant Tortoise) was beyond doubt the most conspicuous and ecologically important member of the Galapagos fauna. It originally occurred on most of the larger islands. Strictly terrestrial, it varies greatly from island to island in many characters including size and shape of shell, and relative lengths of legs and neck, and these differences are correlated with habitat and feeding. Some are grazers, whereas others are browsers. All are now considered to be conspecific but there is considerable doubt as to this allocation (Bacon, 1980). Several of the subspecies are now extinct and others are endangered.

On the large and mountainous islands such as Isabella and Santa Cruz the tortoises inhabit mainly the cooler and moister upland areas. Some populations live at elevations of 1000 m or more, where there is almost continual mist or cloud cover, and vegetation remains succulent even in the dry season. The females migrate to the warmer lowlands to find suitable nesting sites. In these areas there is more sunshine and better soil, a fine textured mixture of volcanic ash and clay.

Courtship and copulation occur during the rainy season months of February, March and April. There is some male rivalry, and subordinate males may be prevented from mating or even courting. Egg-laying seems to be most concentrated at the height of the dry season, September to November. However, there is some laying throughout the entire dry season on Islas Santa Cruz and Pinzon, according to McFarland et al. (1974). Even after arriving in the nesting area the female makes extended search, testing repeatedly for a suitable site where the rocky soil is sufficiently loose and terrain is open to allow sunshine on the nest. A female may produce two or even three clutches in the same season, at intervals of several weeks. There are up to 24 eggs per clutch. Recorded incubation time ranges from 96 days to at least 200 days. Often it is in the range of four or five months, but clutches laid late in the season tend to have a shorter incubation. Hatching generally takes place in the rainy season, December through April. Female tortoises are believed to mature after age 20, and males between 10 and 20 years.

The reproduction and demography of *G. elephantopus* is still poorly known. Available information is mostly summarized by Van Denburgh (1914); Carpenter (1966b); Hendrickson (1966); McFarland (1972); McFarland et al. (1974); Auffenberg and Iverson (1979) and Bacon (1980).

Amblyrhynchus cristatus (Marine Iguana) is a giant iguanid endemic to the Galapagos. It is polygynous, and dominant males control harems of females but the females move freely from one area to another. The food consists exclusively of marine algae and the iguanas venture out from the shore to crop it in the intertidal or subtidal zones, chiefly at low tide. During the reproductive season territorial males abstain from foraging, are on their territories continuously, and may lose as much as 25 per cent of their body weight in six weeks. On Isla Fernandina, males begin to establish territories in late September and their schedule is one month later on Isla Santa Cruz and also on Isla Española, some 330 km farther southeast. Size of a territory varies from 1 to 10 m^2. Copulation occurs in the first three weeks of January on Isla Santa Cruz. Females are believed to copulate only once in a season. Egg-laying occurs about five weeks after copulation and there are normally 2 (1-3) eggs per clutch. For nesting, females migrate from the rocky shoreline to certain sandy beaches and there space is at a premium. A nesting female is highly aggressive toward an intruding female and defends her nest site with agonistic behavior similar to that of a territorial male, charging, butting and biting. The nesting is characterized by frequent squabbles between females, frequent displacement of individuals from burrows that they have started, and occasional destruction of earlier nests by later coming females. After egg-laying and covering of the nest the female may stay beside it and guard it against other females for as much as 10 days on Española, but seemingly such guarding does not occur on Fernandina. Incubation, lasting more than three months, falls entirely within the warmer half of the year, avoiding the *garúa* season of relatively low temperature. Also, egg-laying seems to be timed to follow the lowest tides of the year, when conditions are unusually favorable for foraging, and females have been able to accumulate a supply of fat.

Conolophus subcristatus (Galapagos Land Iguana) was the subject of an intensive three-year study by Werner (in press) on the island of Fernandina. During the *garúa* cold season (May to December) the population is scattered and nonterritorial. In the breeding season the adult population is highly concentrated and adult males become territorial. They arrive in the breeding areas from mid-January through March, and do not defend territories for several weeks after arrival. For the three months that they remain in the breeding areas, they do not feed. Females arrive in large numbers in the same areas about three weeks later than the males, many of which do not control territories. After arrival, each female makes a tour of inspection over the area and settles where the available burrows, food supply and resident male are most attractive. However, most females shift one or more times during the course of the season and hence are inseminated by more than one male. Nonterritorial males, lurking inconspicuously about the fringes of established territories, often catch and inseminate females without attracting notice of the resident male. Rape occurs readily because females average less than half the bulk of males. Some females choose an area that overlaps two male territories, resulting in intensified territorial fighting between the two adjacent males. Fights between neighboring males often last for several hours—as much as eight hours daily when boundaries or a female are in dispute.

By June the breeding season is ended and there is mass dispersal from the territories. Males then have an extremely low level of activity. They defend burrows against other individuals, including females. All or most gravid females of the island migrate in a three- to 10-day trek, for distances up to 15 km, ascending to the volcano rim at 1100 m, and into the 900 m deep crater for egg-laying. The crater's rim and floor are cloudless, but there is an almost permanent cloud belt on the flanks of the volcano between 600 and 900 m elevation. In an area of fumaroles where soil is heated by escaping steam, nest burrows are dug by the thousands, with an average interval between them of only a meter or two. Nest temperatures are somewhat above 30°C and are constant night and day. The clutch varies from seven to 23 eggs. Hatching occurs in October about 3½ months after laying. At the time of hatching the island's population of Galapagos Hawks *(Buteo galapagoensis)* concentrates in the area of nests, preying heavily on the young iguanas. Snakes *(Dromicus)* also prey on the hatchlings. Except in the early weeks after hatching, the ratio of juveniles to adult iguanas is always low, perhaps 1 to 10, or even 1 to 30, depending on the time and place. These large iguanids are believed to require many years (7-10 in females, 11-16 in males) to attain maturity, with a life expectancy of 20 to 40 years.

Two species of *Conolophus* are currently recognized, *C. subcristatus* on the islands Fernandina, Isabella, San Salvador, N. Seymour, Playas and Santa Cruz, *C. pallidus* on Barrington. However, Werner (in press) has indicated that discrete populations differ markedly in characters of size, appearance, and habits, and revision is much needed. Van Denburgh and Slevin (1913) recorded the collecting of several ovigerous *C. pallidus* on the north coast of Barrington Island on 10 July 1906 and 23 October 1905. The latter date indicates a marked departure from the seasonal schedule of *C. subcristatus* on Fernandina. The *C. pallidus* eggs still unlaid in October probably would have hatched in the warmer and wetter part of the year after the *garúa*. This is a pattern that is characteristic of various other iguanines. For instance Wiewandt (1979) found that in *Cyclura stegnegeri* of Mona Island in the West Indies, nearly all digging of nest burrows and laying of eggs takes place in an 11-day period, and hatching, after a three-month incubation, occurred in October and early November, the wettest part of the year.

Tropidurus albemarlensis (Lava Lizard) is one of eight *Tropidurus* species endemic to the archipelago, while other less closely related congeners occur on the mainland of South America. *Tropidurus albemarlensis* was studied on the island of Santa Cruz during January and February by Stebbins et al. (1967). These small insectivorous lizards were found to have a polygynous mating system, with a male territory often encompassing the ranges of one or more females (up to 11). There are usually two eggs per clutch but occasionally three or four. Breeding was at its peak in late January. ". . . in warm, sunny years the lizards may breed from November to the end of March, but if the weather is cool and overcast, breeding may be delayed until January and may last until April." Van Denburgh and Slevin (1913) recorded nesting in May and June. In the cool, moist *garúa* season, activity of adults is much reduced but immatures continue to be active. In this lizard, as in the Marine Iguana, reproduction is timed to avoid the cool weather of the *garúa*.

4. West African Forest and Savanna

Nigeria, Ghana and the Ivory Coast of West Africa are regions of contrast, with grassland and tropical rainforest having distinctive faunas in adjacent areas. Annual precipitation is high but seasonal, with pronounced dry seasons.

Agama agama (Rainbow Lizard), a common and widespread African agamid, has been most thoroughly studied at Ibadan, southwestern Nigeria, by Harris (1964). In that area egg-laying commences about mid-February soon after the onset of the rainy season, and continues until October or November. There are usually five or six eggs per clutch. About two months are required for the eggs to hatch; 14 months are required for the female to attain sexual maturity.

As illustrated in Table 9, *A. agama* undergoes striking changes

TABLE 9. Seasons of egg-laying in *Agama agama*

Site of study	Time of egg-laying	Season of precipitation	Authority
Suacoco, Liberia, 7°5′N	mainly June-July but some year-round	Rainy season 240 mm per month, Apr.-Oct. Dry season Nov.-March, average 60 mm per month	Daniel, 1960
Accra, Ghana, 5°21′N	Feb.-June and Oct.-Nov.	Heaviest Jan.-June and Sept., Oct.	Chapman and Chapman, 1964
Ibadan, Nigeria, 7°24′N	mid-Feb. to Oct.	Hardly any rain in Dec.-Jan. increasing to peak of 460 mm in June	Harris, 1964
Kano, Nigeria, 12°02′N	April to October	Rainless Nov. to Mar., building to peak of 300+ mm in June	Harris, 1964
Gadomurtu, Kenya, 0°01′N	June to Sept. (peak July to early Aug.)	Most comes in "long rains" of summer months; "short rains" are in winter; 2 dry seasons	Marshall and Hook, 1960

in its breeding schedule in response to the varying climatic conditions where it occurs across Africa. Also it seems to undergo change in clutch size, from the five or six eggs stated by Harris (1964) to be usual at Ibadan, where egg production occurs through most of the year, to the "6 to 9" eggs stated to be normal at Suacoco, Liberia, by Daniel (1960) in a more seasonal climate, and according to Marshall and Hook (1960) "usually 10 to 12 per clutch" at Gadomurtu, Kenya, where egg-laying is limited to the wet summer months. Marshall and Hook (1960) indicated close correlation between the breeding cycle and the changing food supply. During the summer season of "long rains" insects were abundant, and the lizards collected usually had full stomachs. The abundance and nutritious quality of the protein-rich insect food was believed to trigger the breeding cycle.

Barbault (1974a, 1974b, 1975a, 1975b) studied the reproductive cycles of various kinds of reptiles in Lamto (6°13′N) of the Ivory Coast. In this humid climate, precipitation is heavy through most of the year, but is minimal (with no rain falling in some years) in the month of January, and with December and February also having less than half the average of other months. In the January dry season the grass savanna is burned annually, with drastic effects upon its fauna, by actual incineration and by destruction of food and shelter. The destructive effects of fire are somewhat mitigated by the interspersion of gallery forest providing a refuge for the savanna animals.

Skinks are prominent in the savanna herpetofauna, especially *Mabuya buettneri, M. maculilabris* and *Panaspis nimbaensis.* In these three species clutch sizes average respectively 9.0, 5.7, and 2.56 eggs, with 1.5, 5.5 and 5.0 clutches per female per year. These skinks require about six months to reach maturity. Reproduction is strictly seasonal. In *M. buettneri* for instance, females that are successful produce two clutches late in the rainy season, in November and December. Adults are already much reduced in numbers before the January burning, and are further decimated by the fire. The young emerge mainly in March and April, when the fire has passed and a new crop of vegetation has started to grow, providing shelter and insect food. If burning is delayed beyond the usual time, it may take a heavy toll of the hatchling skinks. Some females survive to reproduce in more than one season. The number of eggs produced is proportional to the size of the female. On an average savanna area annual egg production of *M. buettneri* amounts to about 73 per ha, and about 18 per cent of the eggs survive to develop into adults by the following October.

In adjacent gallery forest, skinks closely related to those of the savanna, *Mabuya blandingi* and *Panaspis kitsoni,* were found to be strikingly different in their general ecology and seasonal schedules.

M. blandingi is a lacertiform skink of glades and clearings; *P. kitsoni* is a serpentiform burrower in humus of deep forest. In both species there is some breeding throughout the year, but the rate is reduced in the dry season. Clutches average 2.74 eggs in *M. blandingi* with total annual production of perhaps 20 per female, while in *P. kitsoni* corresponding figures are 1.94 and 12. Barbault contrasted the small clutch size in each of these two forest skinks with the larger clutches of their near relatives such as *M. maculilabris* (5.7) and *P. nimbaensis* (2.56) on the adjacent savannas, where reproduction is limited to one part of the year. He found that size of clutch is strongly influenced by size (and age) of female in the savanna dwellers, whereas in rainforest species there is less intraspecific variation in clutch size.

Causus rhombeatus (Checkered Night Adder) is widespread in Africa. At Accra, Ghana, Woodward (1933) kept a female isolated in confinement and she laid successive clutches (averaging 15 eggs) on 20 April, 22 May, 16 June, 13 July, 18 August, 18 September and 14 October. Between clutches the female adder fed voraciously on toads, and underwent sloughing. Fertility was 100 per cent in the first and second clutches, 64.7 per cent in the third, and 55.5 per cent in the fourth; subsequent clutches were all infertile. Unfortunately observations were discontinued after the 14 October clutch, so it is not known whether the female could have maintained her production throughout the year. However, all seven clutches were produced during the rainy season. In parts of Africa having drier climates, the breeding season is doubtless more restricted. Pitman (1974) stated that in Uganda the hatching season extended from mid-November to early January. Broadley and Cock (1975) stated that in Rhodesia egg-laying occurs between October and December, while FitzSimons (1962) stated that in southern Africa mating takes place in early spring and there is normally only one clutch per year.

5. *Southeastern Asia (Malay Peninsula and neighboring islands of Borneo and Java).*

This equatorial region is one of heavy precipitation, with the monsoons in certain months bringing heavier rainfall than occurs at other times of year. A spectrum of habitats, rainforest, river and marsh, and a wide variety of areas more or less altered by human activities and supporting dense human populations are included. The many studies of reptilian reproduction in this part of the world include intensive field projects on each of the following groups: sea turtles, river turtles, rainforest lizards, house geckos, rice field snakes and other terrestrial snakes, a homalopsine water snake, and sea snakes.

Batagur baska ("Tuntong"), a large emydid (carapace length about 51 cm) of rivers and brackish estuaries, contrasts with *C.*

mydas in being a seasonal breeder. Its ecology was studied by Moll (1978) along the Perak River on the west side of the Malay Peninsula. Breeding occurs in September, at the beginning of the monsoon season, and the breeding males are striking in appearance, with head, necks and legs black and iris white. After mating, as the monsoon subsides in November, females aggregate and undertake a mass migration upstream, far beyond the brackish coastal waters. By early December the subsidence of monsoon torrents leaves exposed the large sandbanks where nesting occurs, some 80 km from the river mouth. The mass nesting emergences are nocturnal. The nesting female uses all four feet to dig a body pit that may be as much as 120 cm long; then she excavates a relatively small egg cavity, using one hind foot. Digging and laying requires less than an hour, but covering the nest requires on the average, about two hours. On the average there are 26 eggs per nest, but the female distributes her clutch between several nests. The nesting season extends over about three months. Like other large turtles, *B. baska* has been heavily exploited by humans, especially for its eggs, and its populations have been drastically reduced.

Again, on the island of Borneo, in rainforest at Nanga Tekalit (1°37′N), Inger and Greenberg (1966) followed the annual cycles of 10 species of lizards and made casual observations on several others. Annual precipitation totalled 5669 mm (202 to 930 per month). From a year-round sample of 1451 specimens, *Cyrtodactylus malayanus, C. pubisculus, Draco melanopogon*, and *D. quinquefasciatus* were found to be continuous breeders, with no seasonal change in the size of the testes, nor in the ratio of ovigerous to nonovigerous females. Less complete data were obtained for *Aeluroscalabotes felinus, Gonyocephalus grandis, G. liogaster* and *Tropidophorus brookei*, but these too seemed to be continuous breeders, as gravid females were found in 10 or 11 months despite small samples. *Draco obscurus* and *Mabuya rudis* yielded relatively few data. In all these species egg clutches were found to be small. Two-egg clutches are regular for the geckos *Cyrtodactylus malayanus, C. pubisculus* and *Aeluroscalabotes felinus*, and the flying lizard, *Draco melanopogon*. For other species clutches averaged as follows: 2.71 (1 - 4, N = 62) in *Draco quinquefasciatus;* 3.2 (1 - 4, N = 22) in *Gonyocephalus liogaster;* 3.5 (2 - 5, N = 27) in *G. grandis* and 3.7 (1 - 5, N = 16) in *Tropidophorus brookei.* Inger and Greenberg (1966) compared reproductive patterns in the lizards of Nanga Tekalit with those of closely related kinds in seasonal climates of southern Asia. Those from seasonal climates were found to have their reproduction limited to a brief part of the year—May to July in known instances—and produced relatively large clutches. For six kinds of agamids clutches averaged a little more than 10 eggs, and for seven kinds of skinks they averaged approximately six eggs. In the lizards of Nanga Tekalit abdominal fat bodies were always small (not more than 3% of body weight), and showed little variation in size at different times of the year and in individuals at different stages of reproduction.

Church (1962) studied the reproductive cycles of three Javanese house geckos, *Cosymbotus platyurus, Hemidactylus frenatus,* and *Peropus mutilatus,* at Bandung, 6° S. He found year-round breeding in all, with little indication of seasonal change, and found also that the larger the female the greater the likelihood of its being ovigerous. Abdominal fat bodies are lacking in these tropical geckonines, and the clutch is consistently two eggs.

The timing of egg-laying in forest reptiles was studied by Pongsapipatana (1975) in northeastern Thailand, near 14°N. In this area, December, January and February were almost rainless and June also was relatively dry, intervening between an early and mild rainy season, March to May, and a longer and more pronounced wet season, July through October. Most egg clutches were found in May (5), June (7), July (7), August (14), September (6), October (2), November (3). Egg-laying seemed to be better correlated with soil moisture than with actual precipitation, and most clutches were found when soil moisture was 25 per cent or higher. The eggs found were mainly those of geckos *(Cyrtodactylus angularis, C. intermedius, Phyllodactylus siamensis, Cosymbotus platyurus, Hemiphyllodactylus yunnanensis, Peropus mutilatus)* but also included those of one agamid *(Draco maculatus),* three skinks *(Mabuya macularia, Riopa bowringi, Leiolopisma siamensis)* and a snake *(Liopeltis scriptus).*

In Western Java, DeHaas (1941) made year-round collections of common snakes and studied their reproductive cycles from a total of 3509 specimens examined in a six-months period. At the two localities of the study precipitation was heavy throughout most of the year (monthly means 286 and 345 mm) but with much less in July, August and September. In all the common species for which adequate quantities of data were available, DeHaas found evidence of year-round breeding in the seasonal distribution of ovigerous females and of hatchlings. In the small fossorial colubrine *Calamaria lumbricoidea* he found ovigerous females mainly in the period June through September, but in *C. linnaei* gravid females were almost uniformly distributed throughout the year. In both species young were most in evidence during the last three months of the year, but the trend was stronger in *C. lumbricoidea.* In *Gongylosoma baliodeira* ovigerous females were more abundant in June-July-August-September than at other times. The June sample consisted entirely of adults, but the ratio of young increased sharply through the following months until they made up the majority of the samples in October, November and December. Then their numbers dwindled to 20-30% of the samples during the spring months. In the natricine *Rhabdophis subminiata* the August and September samples consisted entirely of adults, but in subsequent months their ratio to immatures steadily declined, to a minimum of 13% in March, then steadily increased again. In *R. chrysarga* the trends were similar. Gravid females of each of these species were found in every month of the year, with just one exception; no gravid females of *G. baliodeira* were recorded in January.

Bergman (1943) made year-round collections of sea snakes at Surabaia, Java, approximately 7° S. The six commonest species, obtained in substantial numbers (totalling 984), were *Thalassophis anomalus, Lapemis hardwickii, Enhydrina schistosa, Hydrophis brooki, H. fasciatus* and *H. cyanocinctus*. In contrast to the terrestrial snakes and lizards, these six sea snakes were found to be highly seasonal in their reproduction, all with similar trends. Ovarian follicles began to enlarge in March, and reached a peak in June. A few females had enlarged follicles as late as September. Ovigerous females were first found in May but were still few. In July, August and September approximately three-fourths of all adult females were pregnant; thereafter numbers rapidly declined, to none in December. Young averaged only two per litter in *Lapemis hardwickii*, and *Hydrophis fasciatus*, five in *Thalassophis anomalus* and *Enhydrina schistosa*, seven in *H. brooki* and 10 in *H. cyanocinctus*.

In a recent study of sea snakes from four sites along the coast of the Malay Peninsula between 1°41′ and 3°15′N, Lemen and Voris (1981) also found seasonal reproduction but it was out of phase with that at Surabaia. In *Enhydrina schistosa* they found most females gravid, 8 January to 4 February; neonates were abundant in 25 February-13 March samples of this species and *Hydrophis melanosoma*. In *Lapemis hardwickii, Aipysurus eydouxii* and *Hydrophis fasciatus*, gravid females were found chiefly in early March and young of the first-named species were abundant in April. At Muar (2°3′N) they found highly synchronous reproduction (in *E. schistosa*) whereas at Sungai Buloh (3°15′N), *H. caerulescens* and the acrochordid *Acrochordus granulatus* seemed to have loosely seasonal or aseasonal reproduction. This difference suggested a high degree of plasticity in reproductive cycles. In adequately large (N = 7-69) samples of gravid females, they found the following mean numbers of oviducal eggs indicative of litter sizes: *Aipysurus eydouxii* 4.4, *Acrochordus granulatus* 4.3, *Lapemis hardwickii* 3.3, *Thalassophina viperina* 3.5, *Hydrophis brooki* 4.9, *H. caerulescens* 5.9, *H. fasciatus* 3.3, *H. melanosoma* 6.0, *H. torquatus* 5.5, *Enhydrina schistosa* 18.3. Most of the species were considered to be *K*-strategists, with relatively few young per litter and young relatively large (reproductive effort per embryo 4.6 to 10.9 per cent), but *E. schistosa* was considered an *r*-strategist, having large litters of small young (mean effort per embryo 2.1 per cent). Reproductive effort per clutch was found to average 38.9 per cent in *E. schistosa,* 23.6-38.3 per cent in nine other species. Young of *Enhydrina* mature in their second year.

Over a three-year period, Kopstein (1938) examined several thousand snakes of some 15 species, primarily those of rice fields on the Malay Peninsula. The climate was much like that described for Java, with precipitation averaging about 300 mm in most months, but with August and September having only about one-tenth as much, and with May, June and July also below the average. For the common rice field snakes, including *Xenochrophis vittata, Ptyas mucosus, P. korros,* and *Naja naja* egg-laying was found to be concentrated in the winter rainy season. Records were most complete for *Xenochrophis vittata,* and for this common natricine, egg-bearing females were found in every month of the year.

A noteworthy aspect of Kopstein's study was the keeping of confined females to record their reproductive histories. A female of *X. vittata* produced successive clutches of eight eggs each on 26 March and 3 May; another laid on 31 May (5 eggs) and 27 September (6 eggs). Two other females of this species were confined together and their products were not distinguished individually, but in the course of a year their combined output amounted to 11 clutches totalling 48 eggs. A female of *Rhabdophis subminiata* produced clutches on 9 July (5), 2 October (7), and 15 November (5). Another laid on 25 June (9) and 21 August (10). A female of *Boiga multomaculata* laid on 5 May (4) and 1 January (4); another on 22 October and 21 December.

Another important aspect of Kopstein's study was the recording of time from hatching to sexual maturity in individuals of several species; it was remarkably short in some small species. In *Xenochrophis vittata* both sexes were found to attain maturity in 10½ months, and in *Amblycephalus carinatus* 11 months, whereas in the large rat snake, *Ptyas mucosa,* 20 months were required. In *Rhabdophis subminiata* males required 13 months to mature, females 17½ months.

Homalopsis buccata (Puff-faced Water Snake) a venomous, rear-fanged, highly aquatic, freshwater snake was studied by Berry and Lim (1967) at Kuala Lumpur, West Malaysia on the Malay Peninsula near the equator. The region is characterized by extremely high rainfall, 2400-3700 mm annually, with no dry season, and a warm humid climate with mean daily temperature 26°-28° C. The snakes are viviparous, producing litters of 2-20 young ($\bar{x}$ = 9.26). Presumably gestation lasts a little more than three months, as in other viviparous snakes. Pregnant females were present in the samples at all times of year. However, during the half of the year from October to March, the ratio of ovigerous to other adult females was relatively high (60 per cent) whereas during the remainder of the year, April through September, it averaged less than half that (28 per cent). The percentage of juveniles captured was twice as high from April through September as from October through March. Abdominal fat bodies were present in all snakes but were more prominent in adults than in young, and larger in adult females than adult males. In females size of fat bodies showed no obvious correlation either with season or with stage of reproduction. In males both testes and fat bodies changed seasonally in weight in somewhat parallel fashion. The mean weights were relatively high from October to January, then declined to a minimum in April and May, and gradually increased again from June through September.

Discussion and Conclusions

The majority of reptile species are limited to the tropics, and show a great variety of patterns in reproductive cycles. Even in one region or locality, species subject to the same climatic regimes and biotic environments differ widely in their reproductive cycles, each with its special evolutionary adjustments.

A relatively small group of species has been found to breed continuously with no seasonal change. All of these occur in aseasonal climates having high precipitation throughout the year; most are inhabitants of rainforest or cloud forest. A much larger number of species have been found to be more or less continuous breeders that constantly change the level of their reproduction. In most instances that have been studied, amount of precipitation seems to control level of reproduction. The effect may be direct, as in many *Anolis* which respond to sprinkling in the dry season by ovipositing, or it may be indirect as in *Agama agama* in which the rainy season triggers reproduction seemingly through the abundance of nutritious insect food that develops on the new crop of vegetation.

A large number of tropical species have their reproduction limited to one part of the year. For many of these that occur in seasonal climates with drought for part of the year, reproduction is limited to the rainy season(s). There may be a lag from the onset of rains until the beginning of egg production, or the response may be almost immediate. A species may vary its reproductive cycle in different regions, with continuous and regular year-round breeding in an aseasonal climate, continuous but irregular breeding where the climate has some seasonality, and discontinuous breeding where seasonality is more pronounced.

While most kinds of tropical reptiles that have a restricted breeding season seem to have their breeding timed to periods of high precipitation, others, including a variety of aquatic terrestrial and arboreal types, have their reproduction timed to the drier part of the year, e.g. *Crocodylus niloticus, Iguana iguana,* and *Podocnemis expansa,* all of which nest in sandy riverbanks, in sites that are inundated in times of flood. Oviposition occurs at times of falling water level, with the prospect that submergence will not occur until after hatching time.

Although temperature, moisture and photoperiod are the most familiar factors regulating the timing of breeding, other factors including biotic ones may take precedence. For example Kiester (1975) found that the large, viviparous anguid, *Diploglossus millepunctatus* of Malpelo Island off the Pacific Coast of Colombia, seems to have its breeding synchronized with that of the Blue-faced Booby *(Sula dactylatra).* The colonies of nesting boobies provide an important food source for the lizard. It was observed that the arrival at the nest of a parent booby with fish would cause nearby lizards to run toward the nest, and snatch any fish dropped by the birds. At times of year when nestling boobies are not present the lizards are believed to subsist on a relatively meager fare of crabs, carrion, feces and miscellaneous items.

Active and scansorial habits in the progenitors of *Anolis* and the sphaerodactyline geckos doubtless resulted in selection for reduced bulk of egg clutches, and ultimately the single-egg clutch, imposing a relatively light burden with minimum handicapping of the gravid female. A comparable example of the effect of life-style on reproductive strategy is provided by the saxicolous, crevice-living iguanid, *Platynotus semitaeniatus,* having a two-egg clutch. With a single elongate egg in each oviduct, the gravid female is little handicapped in her ability to squeeze into narrow crevices for shelter. Two-egg clutches occur in many crevice-living saxicolous lizards of other families, including geckonine and eublepharine geckos, skinks *(Carlia, Cryptoblepharis, Emoia, Lipinia, Trachydosaurus),* cordylids *(Cordylus, Platysaurus)* and xantusiids *(Xantusia henshawi).* In all these, including the viviparous *Cordylus* and *Xantusia,* the small complement may be an adaptation or preadaptation permitting the female to utilize narrow crevices, with minimal handicapping of egg-bearing individuals.

At the opposite extreme, sluggish and slow-moving reptiles with cryptic color and pattern are relatively little handicapped by the burden of a large egg-clutch. Chameleons, certain iguanids *(Corytophanes, Phrynosoma, Polychrus)* and vipers (both crotaline and viperine) provide some of the best examples. The female's ability to carry a bulky clutch without much handicap to herself and with relative safety to the developing embryos has possibly led to the development of viviparity, several or many times independently, in such primitively oviparous groups as the chameleons, crotalines and viperines. In the members of these groups and others that have retained the oviparous mode of reproduction, the large egg-clutch may render unnecessary the production of two or more successive clutches. Instead, the female is able to time the production of her single clutch optimally to benefit from climatic and biotic factors, and avoid the rigors that might befall her and/or her eggs if their production were less appropriately timed.

Tropical reptiles, largely free from the seasonal constraints that enforce a short breeding season on those of cool-temperate climates, tend to differ from the latter in a suite of interrelated traits. Those in cool-temperate climates are more often characterized by: 1) relatively large female size, 2) large clutches or litters, 3) higher incidence of viviparity than occurs in the tropics, 4) small body size. In contrast, tropical reptiles more often have the opposite conditions of relatively small female size, small clutches (compensated by frequent oviposition), high incidence of oviparity, and sometimes very large body size (but ranging down to very small).

Continuous versus discontinuous breeding are contrasting conditions which in many instances occur in closely related species of reptiles. Discontinuous breeding seems to be more common, but perhaps in past eras when aseasonal climates occurred more extensively, the opposite applied. Actually the transition from either condition to the opposite one has probably occurred many times in the evolution of the world's herpetofauna, taking place with relative ease and rapidity when conditions changed.

The transition from continuous year-round breeding to the discontinuous seasonal type occurs intraspecifically in many reptiles. The geography of the African continent permits many equatorial species to range uninterruptedly into the Temperate Zone at the southern end. For several of these, including *Chamaeleo dilepis, Mabuya quinquetaeniata, M. striata, Boaedon fuliginosus, Lycodon aulicus, Lycophidion capense, Philothammus hoplogaster, P. irregularis, Crotaphopeltis hotamboeia, Dispholidus typus, Psammophis sibilans, Bitis arietans* and *Causus rhombeatus* there is evidence of shift from continuous tropical breeding to seasonal temperate-zone breeding. In each of these there is evidence in scattered records by Loveridge (1929, 1936, 1939, 1940, 1942, 1951, 1953, 1958), Robertson, Chapman and Chapman (1962), Broadley (1959), Pienaar (1966) or Woodward (1933) of continuous breeding somewhere in the tropics, whereas statements by FitzSimons (1943, 1962) indicate that in South Africa these same species produce eggs in spring or early summer (or give birth in late summer or autumn in *Mabuya quinquetaeniata, M. striata,* and *Bitis arietans*). In Asia, desert and mountain barriers prevent the ranges of most tropical species from extending into the Temperate Zone. Year-round breeding of the Javanese geckos *Peropus mutilatus* and *Hemidactylus frenatus* becomes seasonal farther north, so that hatchlings are to be found only in July and August in Japan *(P. mutilatus)* and the Loo Choo

Islands (*H. frenatus*, Fukada, 1965). The viviparous skink *Lipinia noctua* was found to bear only one young at a time in the tropics of New Britain (Hediger, 1934), but most frequently bears two in Hawaii (Oliver and Shaw, 1953). The Indian rat snake *Ptyas korros* was found by Kopstein (1938) to be gravid at all times of year in the tropics of the Malay Peninsula, but in the temperate climate of China was found by Pope (1935) to be gravid only in late May and early June. The Jamaican anoles, *Anolis grahami* and *A. sagrei* were found to have some reproduction year-round, but their reproduction is arrested for nearly half of the year in the cooler winter climates of Bermuda *(grahami)* and southern Florida *(sagrei)*.

Pseudemys scripta has a relatively long breeding season in the tropics (Panama) but a much shorter season in the Temperate Zone of the United States (see p. 23). Occurring sympatrically with *Pseudemys scripta* in the Panama Canal Zone, *Kinosternum leucostomum* is a continuous breeder, and normally lays only one remarkably large egg at a time, and the incubation period is lengthy —up to five months. *Rhinoclemys funerea,* also sympatric in the same area, differs from *P. scripta* in extended breeding season, few and relatively large eggs, and long incubation. Moll and Legler (1971) considered *K. leucostomum* and *R. funerea* to be typical of tropical turtles in their reproductive patterns, but they considered seasonal reproduction in *P. scripta* with large clutches of small eggs to reflect recent arrival in the tropics, where its success could be attributed to the finding of an unoccupied niche. However, the South American *Podocnemis* and the Asiatic *Batagur* presumably representing 'old tropical' elements of the fauna, also have large clutches and seasonal reproduction. The reproductive patterns of both *K. leucostomum* and *P. scripta* have their analogs in tropical lizards and it cannot be stated that one is better adjusted than the other to tropical conditions. It was shown (p. 29) that in the South American rainforest, small lizards that produce only one or two eggs at a time are likely to be continuous breeders whereas large kinds that produce many eggs in a clutch are usually discontinuous breeders and may lay only one clutch annually. Probably there are similar trends in turtles and in snakes.

Intraspecific geographic and local differences between populations may be enforced by differences in habitat, food supply and/or sociological factors, even though they may lack genetic bases. The giant tortoises *(Geochelone gigantea)* of Aldabra Atoll, 9°24′S in the Indian Ocean (studied by Swingland and Coe, 1978) provide an example. Like their Galapagan relatives, tortoises of Aldabra copulate in the rainy season (from February to May) and nest entirely within the dry season (June-September). The young emerge just before the next rainy season, or after its onset. The Aldabran tortoises show significant demographic differences on the several islets where they occur, seemingly occasioned by population pressures and limited food supplies. On Malabar, with relatively low population density, maturity is attained relatively early (female 17 years, male 20), female size is relatively large, egg size is relatively large, eggs average 11 to 14 per clutch, and each female lays several clutches per season. On Grande Terre maturity is delayed (female 23 years, male 26), female size is only half that on Malabar, females do not breed annually, egg size is relatively small, a female produces only one clutch in a season, with 4 to 6 eggs, and atresia of many preovulatory follicles.

In the Basilisk *(Basiliscus basiliscus),* a large, semi-aquatic iguanid, similar demographic divergence is illustrated in neighboring populations along the Río Corabicí and Río Sandillal, in northwestern Costa Rica (Van Devender, 1978). The Sandillal is small and sluggish with muddy banks and bottom; the Corabicí is relatively large, swift and rocky. Study areas were only 2.5 km apart, and the two watercourses are confluent a short distance downstream. At both sites females reach sexual maturity at about 135 mm (SVL) and at an age of 20 months, but male growth rate and maximum size differ between sites. Adult males were usually 167-176 mm at Río Corabicí vs 213-238 mm at Río Sandillal. At the latter locality immature and small mature males are constantly harassed by large, dominant individuals, and have little opportunity for successful courtship. Their best strategy is to avoid dominant males, forego reproduction, and grow as rapidly as possible. At the Río Corabicí the ratio of females is higher, male growth is slower, and there is a paucity of large, dominant males. With less harassment and more opportunity for courtship, small males can afford to divert more energy from growth to reproductive activity.

At both sites reproductive activity begins with the rainy season, remains at a high level for seven to eight months and increases at the beginning of the dry season, then stops for the remainder of the dry season. Flooding of nests was found to be a major cause of egg-mortality, with 14% egg survivorship at the Corabici and only 4% survivorship at the Sandillal.

In summary, tropical reptiles have diverse reproductive patterns that are highly attuned to local environments. At any locality where there are many sympatric species, each differs somewhat from all others in the nature and timing of its reproductive cycle. Species that are wide-ranging usually are subject to geographic changes in reproductive traits such as size of clutch, timing of breeding season, and time required to attain maturity. In some instances geographical differences reflect genetic divergence that has arisen through natural selection in adaptation to specific environments, but in other instances local demographic traits seems to be non-genetic and determined by capacity of the individual to respond appropriately to local conditions that may include food supply, weather, or sociological factors.

The amount and timing of precipitation is one of the chief controls for reproductive cycles. Reproduction may be triggered either indirectly by the shelter or food supply that result from rain, or directly, by the moisture itself. In contrast to the many rainy-season breeders, there are, in the same communities, a smaller number of dry-season breeders, notably those turtles, lizards and crocodilians that depend upon riparian sandbanks for nesting sites. In the relatively aseasonal climate of a tropical rainforest, a common pattern, especially in the smaller kinds of lizards, is the frequent and more or less regular production of small clutches throughout the year, or most of it. On the other hand, many tropical reptiles, especially larger kinds, produce only once in the annual cycle. The complexes of interrelated factors that affect reproductive cycles include some that are fairly obvious, such as temperature and moisture requirements, and others that are much more subtle and difficult to identify, including specific "life-styles" with special strategy for food-getting or escaping enemies. An example of the latter is the flattened body shape and utilization of rock-crevice escape shelters in certain saxicolous lizards, with associated two-egg clutch and altered egg shape, permitting the gravid female to continue to utilize crevices effectively, but necessitating compensatory frequent production of clutches. Among the more remarkable reproductive cycles that have been evolved are the one-egg clutches of anoles and sphaerodactyline geckos, with many ovipositions over a long breeding season; and the relatively enormous ($>$ 100) clutches of sea turtles, several laid within a few weeks, but with intervals of two or more years intervening between such egg-laying episodes. Reproductive cycles are labile, rapidly evolving, and readily altered by natural selection. Nevertheless, there are patterns that are characteristic for species, genera and higher taxonomic categories.

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