

## REPRODUCTIVE STRATEGIES OF REPTILES

Henry S. Fitch

The word strategy is derived from the Greek, *strategos* — a general; originally with military connotation, it meant a trick or deception to deceive or surprise the enemy. By extension, strategy applied also to politics, business, and courtship, always involving an opponent and a plot to deceive him or her. In contrast, the term is now used by biologists in a looser sense; a species' "reproductive strategy" is merely the most efficient means for it to reproduce and survive, and there is no specific opponent nor planned deception.

This less precise biological meaning that is now in general use, seems to have evolved through several stages. The term "feeding strategy" was first applied for a predator pitted against its prey, later it was extended to include nonpredatory feeders (Schoener, 1971), and, still more recently, to reproduction (Ballinger, 1977).

Although the term reproductive strategy has come into use only recently, the concept of adaptation that it involves is not new. In the *Origin of Species*, Darwin (1859) described many reproductive adaptations. Among biologists of the early part of the present century Joseph Grinnell (1914) of the University of California merits special mention. He discussed reproductive adaptations and compared reproductive potentials not only in his scholarly publications but in his class lectures. He was a pioneer in developing the concept of the ecological niche, and he thought of the species' reproductive traits as aspects of the niche.

Reproductive strategies involve many sorts of adaptations. Mating systems, time from hatching or birth to maturity, span of reproductive life, retention of oviparity or

assumption of viviparity, size of clutch or litter, interval between successive broods, sex ratios and relative sizes of male and female are all important aspects of these adaptations. The timing of various events in the reproductive cycle involve adaptations to climate, and to biotic associates that provide food or shelter varying in quality or amount at different times of year.

Presumably breeding is timed in each species to gain maximum benefits from favorable weather and food sources, and to avoid the harsher aspects of the environment at critical stages in the life history. Hence in the Temperate Zones most species of reptiles breed in spring soon after emergence from hibernation, and hatchlings or neonates appear in the latter half of the growing season, when vegetation and animal life are relatively abundant providing ample food and shelter.

In the tropics where temperature change during the annual cycle is slight, most species of reptiles concentrate their breeding in the wetter parts of the year, and reproduction ceases altogether or declines to a relatively low level in the dry season(s) (Kopstein, 1938; De Haas, 1941; Baker, 1947; Marshall and Hook, 1960; Licht and Gorman, 1970). As a result eggs are at minimum risk from desiccation, and hatchlings emerge at a time of year when food sources in general are abundant.

Actually, this common pattern of rainy-season breeding in tropical reptiles has many exceptions, notably in those kinds that excavate nests for their eggs in riparian sandbars. *Crocodylus niloticus* (Cott, 1961), *Podocnemis expansa* (Roze, 1964), and *Iguana iguana* (Fitch and Henderson,

1977) among others oviposit early in the dry season, when receding waters have left exposed sand banks, with the prospect that flood waters will not inundate them again for several months — not until after the eggs have hatched. The young emerge early in the rainy season.

A less typical strategy is that of the large viviparous, anguid lizard *Diploglossus millepunctatus* of Malpelo Island, Colombia, which seems to have its reproductive cycle timed to that of the Blue-faced Booby colonies there. Fish brought by the parent boobies to their young, and dropped at the nest, provide an abundant food source for the lizards, but when nestling boobies are not present, the lizards must depend on a relatively meager fare of crabs, carrion, feces and miscellaneous insects (Kiestler, 1975).

The names of Eric R. Pianka, Donald W. Tinkle and their co-workers are associated with the recent surge of interest in reproductive strategies. Tinkle *et al.* (1970) recognized two contrasting strategies in the lizard species they studied: (1) early maturing, multiple brooded, and (2) later maturing, single brooded. Pianka (1970a) further developed the concept of *r*- and *K*-selection which has become such a preoccupation with ecologists during the past decade, and he was the first to apply it specifically to reptiles. In *r*-selection emphasis is on the ability to reproduce rapidly and copiously, to exploit favorable conditions in a generally unstable and fluctuating environment. Life expectancy is short, broods are large, and "semelparity" [reproducing only once] is common. Incidentally, no reptile species is known to be semelparous. In contrast *K*-selection is characteristic of more stable environments and emphasizes survival of the individual, with postponed maturity and relatively small broods of young, but with iteroparity [reproducing repeatedly] and sometimes with parental care and/or viviparity.

Obviously there is some parallelism between the reproductive types described by Tinkle *et al.* (1970) and those that exemplify *r*- and *K*-selection. With rapid accumulation of new information concerning the reproductive biology of numerous reptile species, it has become abundantly clear that reptiles in general do not show a well marked dichotomy along the lines of *r*- and *K*-selection nor between early-maturing, multiple-brooded and late-

maturing single-brooded extremes. Instead, almost every species studied has turned out to possess some combination of traits that render its categorizing equivocal in either system. Collectively, these or any random group of reptile species might form a virtual continuum between the extremes postulated either by the *r*- and *K*-concept or the two types of Tinkle *et al.* (1970).

Among living reptiles those that are the best examples of *K*-selection, and Type 2 of Tinkle *et al.* (1970) with low reproductive potential and long life expectancy, are several of the large- to giant-sized species that have evolved on remote oceanic islands: *Sphenodon punctatus* in New Zealand, *Geochelone elephantopus* of the Galapagos, *G. gigantea* of the Seychelles, and the iguanines *Amblyrhynchus* and *Conolophus* of the Galapagos and *Cyclura* species of the West Indies. All these require several years to attain maturity, and then produce only small clutches of eggs. Such evolutionary adjustment to environments almost free from natural enemies of course rendered them particularly vulnerable to change. The arrival of man and feral mammals heralded rapid reduction or local extinction in almost every instance.

Except in the refugia of these oceanic islands, the world's giant reptiles are *r*-selected, at least in their very large clutches and in the relatively small size of their hatchlings. *Chelonia mydas*, as an extreme example, often produces more than 100 eggs per clutch, and produces up to eleven clutches per season (Pritchard, 1967). However, it should be noted that such egg-laying episodes are not annual events for the individual female, but occur every second, third or fourth year depending on the population involved. Anyhow, all of the world's largest reptile species, including sea turtles, crocodylians and pythons, are extremely prolific. However, large and giant-sized reptiles all require several years (up to 20, minimum 2) to attain sexual maturity.

At the opposite extreme, in having short generations, are various small lizards including iguanids, teiids, and lacertids, which have high rate of reproduction and rapid population turnover. *Anolis humilis* (Fitch, 1973), *A. limifrons* (Fitch, 1973), *A. oculatus* (Somma and Brooks, 1976), *Crotaphytus collaris* (Fitch, 1970), *Uta stansburiana* (Tinkle, 1967), *Sceloporus undulatus* (Tinkle and Ballinger, 1972), *S. olivaceus*

(Blair, 1960), *S. variabilis* (Fitch, 1970), *S. chrysostrictus* (Fitch, 1970), *Cnemidophorus deppei* (Fitch, 1970), and *Takydromus tachydromoides* (Telford, 1969) all exemplify both *r*-selection and Group I of Tinkle *et al.* (1970). These lizards may attain sexual maturity in less than four months (exclusive of time spent in hibernation by the Temperate Zone species). Subsequent egg production is rapid (with frequent laying or large clutches or both) to compensate for high mortality rates at all stages of the life history.

Some of the most significant trends in reproductive strategies are intraspecific, in species that vary geographically over extensive ranges. Relatively few polytypic species have been investigated in their reproductive biology in different parts of their ranges, but such studies, when made, have been highly rewarding.

Time required to attain maturity and produce gametes, interval between clutches,

number of eggs per clutch, and size of hatchling or neonate are all important aspects of the reproductive strategy, and every one of these items has been found subject to geographic variation. Such geographic change may either be genetic or it may be due to the direct effect of the environment on the individual. For example, in a northern climate the short growing season might allow time for production of only one clutch in an animal genetically capable of producing two. However, in most instances there are probably genetic differences that result from evolutionary adjustment to local conditions.

Many of the intraspecific changes in reproduction that have been noted seem to have a latitudinal basis. Several of these are illustrated in Tables 1 and 2.

The southern populations of these eleven reptile species in Table 1 produce broods that average slightly more than half the numbers produced by their northern coun-

Table 1. Reptile Species In Which Clutch or Litter Size Has Been Shown To Decrease From North to South

Species	Mean brood size in north	Mean brood size intermediate	Mean brood size in south	Authority
<i>Sternotherus odoratus</i>	4.6 N. U.S.		2.2 S. U.S.	Ernst and Barbour, 1972
<i>Chrysemys picta</i>	10.7 Wisconsin		4.1 Louisiana	Moll, 1973
<i>Malaclemys terrapin</i>	9.7 New Jersey		6.6 Florida	Seigel, 1978
<i>Trionyx spiniferus</i>	19.6 near lat. 40°N.		9.6 south lat. 36°S'	Webb, 1962
<i>Trionyx muticus</i>	20.7 near lat. 40°N.		7.3 south lat. 36°S'	Webb, 1962
<i>Sceloporus graciosus</i>	6.0 N. Utah		3.8 S. Utah	Burkholder & Tanner, 1974; Tinkle, 1973
<i>Sceloporus undulatus</i>	11.8 Ohio		7.6 Georgia	Tinkle & Ballinger, 1972; Crenshaw, 1955
<i>Scincella lateralis</i>	3.8 Kans., Mo.	2.9 Okla., Ark.	2.6 Florida	Fitch, 1970; Brooks, 1967
<i>Heterodon platyrhinos</i>	25.1 N. U.S.		22.1 S. U.S.	Platt, 1963
<i>Agkistrodon contortrix</i>	6.2 N. E. states	5.0 Kansas	3.0 W. Texas	Fitch, 1970
<i>Crotalus viridis</i>	11.3 2 northern tiers of states	7.5 Col., Ut., Nev.	7.0 Ariz., S. Calif.	Klauber, 1956

Table 2. Reptile Species In Which Clutch Size Has Been Shown To Increase From North To South

Species	Mean brood size in north	Mean brood size intermediate	Mean brood size in south	Authority
<i>Chrysemys scripta</i>	9 Illinois		17 Panama	Cagle, 1950; Moll & Legler, 1971
<i>Crotaphytus collaris</i>	5.8 Kansas	6.4 Arkansas	7.2 Texas	Fitch, 1970; Trauth, 1978
<i>Holbrookia maculata</i>	5.0 Nebraska, Kansas		7.0 N. Mexico	Fitch, 1970
<i>Uta stansburiana</i>	2.7 N.W. states		3.4 S. Calif. & Baja Calif.	Fitch, 1970
<i>Cnemidophorus sexlineatus</i>	2.7 Kansas	2.9 N. Car.	3.1 W. Texas	Fitch, 1958; Brown, 1956; Hoddenbach, 1966
<i>Gerrhonotus multicarinatus</i>	9.0 Oregon	11.6 N. Calif.	12.6 S. Calif.	Fitch, 1970
<i>Diadophis punctatus</i>	3.5 Michigan	3.9 Kansas	5.2 Florida	Blanchard, 1930; Fitch, 1975; Myers, 1965

terparts. However, in each of the turtles and lizards the investigators found, or at least suspected, that more than one clutch per season was produced (up to six clutches) by females of the southern populations. In most of the species the total egg production per female per year was greater in the southern populations. In both the *Trionyx* species it was found the clutches of the southern turtles, with fewer eggs, averaged slightly larger than the clutches of their northern representatives with more eggs. In the three snake species the smaller brood sizes to the southward are not compensated by more frequent broods. *Heterodon platyrhinos* normally produces one clutch per year. In the two crotalids viviparity, with a long gestation period, prevents production of more than one litter in a season. Insofar as known, females of both species produce litters in alternate years. In both species there are populations of large individuals in the northern parts of the range and small individuals in the southern parts, possibly with a general trend. Furthermore, neonates differ less in size than do adults; that is, the relatively few neonates of the small, southern snakes are born relatively large paralleling the trend of egg size in *Trionyx*.

As in birds (Lack, 1966), photoperiod may have important effects on reproduction. For diurnal species the long summer days at high latitudes may promote maximum food consumption, with high metabolism and maximum egg production.

Besides the increased number of eggs per clutch in these species, there is a general trend of increase in number of clutches per season — from only one clutch in the north to two or more clutches farther south (up to six in Panamanian *Chrysemys*). The total output of eggs is hence greatly

increased, as much as nine fold in *Chrysemys*. In most of the species increased clutch size is correlated with increased body size southward. However, no such change has been demonstrated in *Cnemidophorus sexlineatus*. In *Diadophis punctatus* the latitudinal gradient is reversed; the Florida snakes are only a little more than 70% of the length of the Michigan snakes while those from Kansas are intermediate (87%).

It is uncertain whether all the species included in Table 1 and 2 actually have latitudinal trends in brood size, and many additional samples are needed to clarify the extent and direction of their variation. Table 3 (adapted from one published by Goldberg, 1976) shows geographic variation in clutch size in *Cnemidophorus tigris*, a species intensively studied in various parts of its wide range. Each figure for mean clutch size is based upon a substantial sample. Obviously clutch size varies geographically but the trends are not very clearcut and do not indicate latitudinal clines. In most of the studies that have been made of *C. tigris*, number of clutches per season was not definitely determined, but it seems that those populations having the largest clutches (in the San Gabriel Mountains, in Idaho, and in Colorado) are single-brooded, whereas those populations having the smallest clutches (Arizona, New Mexico, Texas) often have two clutches per season, or perhaps more. Time from hatching to maturity is another important variable within this species, and some investigators have presented evidence that sexual maturity is attained in the second year whereas others have found maturity postponed until late in the third year. Various combinations of all these variables render the reproductive strategy of *Cnemidophorus tigris* quite different in different parts of its range.

Table 3. Mean Clutch Size in *Cnemidophorus tigris*

Mean clutch size	Geographical origin	Authority
4.1	San Gabriel Mts., S. Calif.	Goldberg, 1976
3.4	Colorado	McCoy & Hoddenbach, 1966
2.9	S.W. Idaho	Pianka, 1970b
2.7	S.W. Idaho	Burkholder & Walker, 1973
2.6	S. Arizona	Pianka, 1970b
2.4	W. Mohave Desert, Calif.	Pianka, 1970b
2.3	S. Nevada	Pianka, 1970b
2.2	Winkler Co., Texas	McCoy & Hoddenbach, 1966
2.1	S. Arizona	Parker, 1972
2.0	Lower Colorado River	Vitt and Ohmart, 1977
2.0	S. Central New Mexico	Medica, 1967

A striking case of variation in clutch size that is not a latitudinal cline is that of *Coluber constrictor*, with means of 16.8 eggs in the northeastern United States, 11.6 in Kansas and 5.8 on the West Coast (Fitch, 1970). Reduction in clutch size accompanies reduction in body size, and the far western racers are only about 70% of the length of the eastern. Somewhat parallel change in clutch size and body size had been found in the relatively small available samples of *Lampropeltis triangulum*; 17 clutches from the eastern United States average 12.9 (6-26) eggs, whereas 10 clutches from Kansas and Iowa average 6.7 (5-8). In the western red milk snakes, with small clutches (*L. t. sypila*) maximum length is only 67 per cent of the eastern (*L. t. triangulum*; Wright and Wright, 1957; Fitch and Fleet, 1970).

Pianka and Parker (1975) discussed the interaction of factors such as those mentioned above, in the reproductive strategy of reptile species. They pointed out that reproductive strategy is altered somewhat during the lifetime of the individual. Thus "primiparae", females producing their first clutch or litter, have relatively few offspring in virtually every reptile species that has been studied. This is correlated with the relatively small size of primiparae, and the fact that they still may be channeling much of their energy into growth. In terms of reproductive effort — biomass ratios of clutch or litter to female — primiparae may or may not equal or exceed females of other age classes. Pianka and Parker (1975) noted the changing reproductive potential, and consequent changing value to the species, of an individual during its ontogeny, as life expectancy declined. Reproduction involves risks and costs to the individual. There is a trade-off between present progeny and expectation of future offspring in terms of costs and profits to lifetime reproductive success. The trade-off is especially complex in those species and populations which produce more than one clutch or litter per season. Compared with first clutches, those following later in the season may have either fewer or more eggs, these may be smaller or larger, and the interval between layings may lengthen or shorten, depending on a variety of factors, both extrinsic and intrinsic.

Although reproductive strategies have a genetic basis, they are also controlled by environmental factors. Under conditions of extreme drought, in desert climates, reptiles that normally have an annual breeding season may skip one or more years, as has been noted for *Sceloporus orcutti* (Mayhew, 1963), *Uma notata* (Mayhew, 1966a) and *U. scoparia* (Mayhew, 1966b). Conversely, unusually high precipitation, and the increased food supply that results, may accelerate reproduction, with earlier maturity and more frequent clutches than usual, as found in *Gambelia wislizenii* in Nevada by Turner, Lannom, Medica and Hoddenbach (1969). The capacity to respond promptly and appropriately to climatic extremes is, of course, an important aspect of reproductive strategy.

It is satisfying to classify and categorize, to determine that one clutch, or two, or three is normal for a species, or that sexual maturity is attained in a given number of years. However, aspects of the life history are often not so clear-cut in nature, and a local population may be divided into two categories, e.g. those that mature in one year, and those that mature in two years. For instance, at the University of Kansas Natural History Reservation I found (Fitch, 1970) that 40% of second-year female red-sided garter snakes (*Thamnophis sirtalis parietalis*) reproduce, whereas attainment of maturity is postponed in the balance of the female population. With respect to time of maturity, northeastern Kansas would seem to be a transitional region from a norm of two years farther south to three years farther north. Any geographic cline in the ratio of the two categories, based on genetic change, would almost surely be altered in its expression from year to year by changing weather, food supply and other environmental factors. Many, and perhaps most, wide-ranging reptile species have such critical transition zones, where there is vacillation in number of clutches produced, in time required to attain maturity, or in number of eggs or young. The tremendous increase or reduction in reproductive potential implied by any one of these changes might result in transition from abundance to rarity, or might impose an invisible barrier beyond which productivity could not

compensate for normal mortality factors. In instances where the population density tapers off gradually toward the range limits, such intangible barriers may be suspected.

Although details of reproductive biology remain poorly known in most reptilian species, it is evident that natural populations have a great deal of genetic diversity. Some of the traits most readily altered by natural selection are those involved in reproductive strategy. As an outcome of the great interest that has developed in recent years in the keeping and breeding of reptiles, it can be predicted that domesticated stocks will be developed. Whether these cage-bred animals will be more attractive than nature's original products may be debatable; but for what they are worth rare mutants including albinos and a potpourri of color and pattern aberrations will be preserved in inbred strains.

Along with such transformations in

appearance, will come a variety of other changes including those of temperament, and reproductive physiology. Even without conscious selection on the part of the keepers, the original traits of a species will tend to be altered in the following ways: 1) Generation time will be shortened, for instance, from two years to one, or from three or four years to two; 2) Captives will become less exacting in their requirements for mating; 3) Fertility will be increased, with more eggs per clutch or young per litter; and 4) Interval between clutches or litters will be shortened. These are trends that are well known in most domesticated animals (Darwin, 1868). Thus captivity will result in intensive selection, molding the animal in a manner quite different from that followed in its natural environment. The final product will be an animal much better adapted to live in close association with humans, in the home or laboratory, but less well adapted for life under natural conditions.

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