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# The Slider Turtle in the Neotropics: Adaptation of a Temperate Species to a Tropical Environment

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## Abstract

The slider turtle, *Pseudemys scripta*, is a polytypic species of North Temperate origin that has established itself widely in the American tropics. Flexible in habitat and dietary requirements, tropical sliders generally grow larger than temperate ones because of longer growing seasons and year-long productivity of warm tropical environments, but growth processes are similar. Tropical sliders have greater reproductive potentials, larger eggs, and longer nesting seasons than temperate sliders, but characteristics and timing of gonadal cycles are similar. Available reproductive data concerning Old World batagurines suggest that tropical sliders have not evolved reproductive strategies similar to their closest tropical aquatic and semiaquatic relatives. Available evidence suggests the likelihood that tropical races of *P. scripta* are Pleistocene immigrants into the tropics and that their successful establishment and rapid dispersal are more attributable to generalized habits than to specific adaptations to tropical environments.

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## Introduction

*Pseudemys scripta* is a polytypic species of temperate origin that ranges from southern Michigan in the United States, sporadically through the American tropics, and, if neotemperate forms are conspecific (Carr, 1952), across the Tropic of Capricorn into temperate Argentina—the most extensive range of any nonmarine chelonian. The obvious success of this turtle in coping with the diverse array of environmental conditions encountered over such a vast range makes its ecology and biogeography of considerable interest.

The lowlands of the American tropics are commonly viewed as the stronghold of the specialist, with available niches filled to capacity by a multiplicity of species (Pritchard and Trebbau, 1984). Under such circumstances the chances for successful colonization by a generalized, temperate-adapted species would seem slight indeed. However, the late Cenozoic was a period of extensive, rapid, and repeated environmental and geological change in the Neotropics, when specialized, resident species may have been at a disadvantage—and particularly vulnerable because of the linkage of the continents via the Panamanian isthmus. Many northern vertebrate species, including *Pseudemys scripta*, successfully invaded and established themselves in the tropics at this time (e.g., see Simpson, 1950; Myers, 1966; Savage, 1966; Duellman, 1979; Pritchard and Trebbau, 1984). Slider turtles, in fact, probably dispersed into the Neotropics as recently as the Pleistocene (Savage, 1966). The objective of this chapter is to examine the ecology of this species in its modern tropical habitats and elucidate its successful strategy for survival as a component of the modern Neotropical fauna. This will entail comparing the ecology of Neotropical sliders with that of North Temperate slider populations that presumably possess the ancestral traits of the group, as well as with that of other emydids known to have had a long-term evolution in the tropics. These comparisons may lead to a better understanding of the degree to which a generalized ecology or specific adaptation to tropical environments explains a population's successful colonization of the American tropics.

Realization of these objectives is hampered by the dearth of studies and information concerning the ecology of *Pseudemys scripta* in the American tropics. The early naturalist-explorers of the Neotropics were mainly collectors, and the work resulting from their collections was largely taxonomic in nature. An exception is provided by the observations of Sumichrast in 1880 and 1882 (summarized in Smith and Smith, 1979) concerning the natural history of *P. s. grayi* in habitats on the Pacific slope of Mexico's Isthmus of Tehuantepec. Breder (1946) provided some ecological information concerning *P. scripta* in the Río Chucunaque drainage of Darien, Panama. The most extensive study of Neotropical slider turtles to date, and the foundation of the conclusions presented in this chapter, was conducted from March 1964 through July 1968 (including field studies conducted on the Río Chagres at Juan Mina, Panama Canal Zone, July 1965–August 1966) by Moll and Legler (1971). Other information concerning Mexican and Central American slider ecology is available in the work of Casas-Andreu (1967), Smith and Smith (1979), Alvarez del Toro (1982), and Vogt (see Chapter 13) for Mexico, and Drummond (1983) and D. Moll (1986) for Central America. The ecology of South American populations has received attention from Medem (1962, 1975) and Pritchard and Trebbau (1984).

### Present Distribution in the Tropics

The slider turtle's distribution in the tropics is sporadic from the Tropic of Cancer southward through Mexico and Central America along the Gulf, Caribbean, and Pacific coasts (Moll and Legler, 1971; Smith and Smith, 1979). Sliders may be encountered wherever suitable habitat becomes available (see Habitat Requirements, below; for Mexican range maps, see Smith and Smith, 1979). *Pseudemys scripta nebulosa*, also technically a tropical slider at the southern tip of its range, inhabits pools in intermittent streams of Baja California. Subspecific designations for these populations are unclear in some cases and have been discussed in some detail by Moll and Legler (1971), Smith and Smith (1979), and Pritchard and Trebbau (1984). Legler (see Chapter 7) provides a more recent analysis. In tropical South America this species' distribution pattern is discontinuous with populations in Colombia, Venezuela, Brazil, and possibly Paraguay and Bolivia. South Temperate populations exist in Argentina and Uruguay, although some investigators consider these a separate species, *P. dorbigni*. Pritchard and Trebbau (1984) discuss their distribution, zoogeography, and taxonomy in detail.

### Habitat Requirements of Tropical Sliders

Moll and Legler (1971) have described ideal habitat for tropical sliders as follows: (1) relatively large, permanent, slow-moving or lotic bodies of water with associated backwaters or small tributaries, (2) large amounts of aquatic vegetation, especially submergent, (3) periodic open or cleared areas in fringing forest (as opposed to solid forest), and (4) abundant basking sites. The lack of one or more of these requirements does not necessarily exclude *P. scripta* from a particular habitat, however, as their tolerance of variation is broad indeed. Tropical sliders may be encountered almost anywhere there is permanent water, and dense populations may exist in apparently barren habitats containing limited resources. Moll and Legler (1971) described one such population from a small muddy Panamanian pond where there was essentially no aquatic vegetation or basking sites and where mud was the primary food source. At the other extreme, sliders may live in brackish-water habitats such as mangrove swamps and estuaries, as observed by J. M. Legler and J. L. Christiansen in Mexico and by Legler in Honduras (Moll and Legler, 1971).

Unbroken rain forest seems to be one of the most difficult habitats for *P. scripta* to colonize, probably because of the difficulty in finding suitable (i.e., relatively open) nesting sites (Moll and Legler, 1971; Pritchard and Trebbau, 1984). Even so, a few rain-forest populations exist in Central America. Pritchard and Trebbau (1984) presented evidence that some of these populations may be

using sea beaches as nesting sites in a fashion similar to that of the Asian beach-nesting emydid *Callagur borneoensis* (Dunson and Moll, 1980), but there is not yet enough information to determine the extent of this behavior in *P. scripta* or the degree of success in hatching or hatchling survival from such nests. If this behavior is truly a genetically fixed population characteristic, then it may be considered a real adaptation to a tropical habitat, because beach nesting is unknown in temperate populations. Alternatively, beach nesting may simply be another example of flexibility allowing *P. scripta* to cope with unfavorable habitats or environmental conditions.

Tropical *P. scripta* appear to benefit from certain types of habitat alteration. Moll and Legler (1971) considered the Río Chagres to be better habitat for sliders after dams slowed and widened the river than before they were built about 1910. Also, populations occurring in forested areas of Panama nested only in areas such as golf courses and abandoned citrus groves, whereas nesting and nests were never observed in dense forest. This is supported by the observation of Breder (1946) that Río Chucunaque populations nested only in areas devoid of vegetation cover. Open areas near aquatic habitats seem to be as close to an inflexible habitat requirement as any possessed by *P. scripta*.

Within a given habitat, juveniles and adults are segregated to some extent (Moll and Legler, 1971; D. Moll, 1986). Three main microhabitats were identified in Moll and Legler's study area in Panama. Hatchlings were generally restricted to the edge of floating mats of grass in lagoons and backwaters of the Río Chagres, larger juveniles were associated with open, lotic situations where thick mats of submergent vegetation were prevalent, and sexually mature adults were in fluvial portions of the river, associated with mats of *Elodea*. *Pseudemys scripta* studied in a slow-moving stream in Belize by D. Moll (1986) displayed similar ontogenetic preferences.

With the exception of the possible beach-nesting behavior in some tropical sliders, there is essentially nothing in the literature to indicate any particularly unique adaptations in habitat usage in the tropics. The description of ideal tropical slider habitat by Moll and Legler (1971) could as easily characterize ideal temperate slider habitat as well (see Carr, 1952; Ernst and Barbour, 1972; Morreale and Gibbons, 1986). Furthermore, temperate sliders can exist and even thrive in such barren habitats as roadside ditches and stock ponds (Cagle, 1950), desert streams (Carr, 1952; Smith and Smith, 1979), and polluted rivers (Moll, 1977). Similar ontogenetic shifts in habitat usage are also known in temperate *P. scripta* populations (Moll, 1977; Hart, 1983). The generalized behavior and broad habitat tolerance of this species, without specific genetically fixed adaptations to local conditions, have probably been key factors in its successful exploitation of the tropics.

### Size and Growth in Tropical Sliders

Mean and maximum sizes attained by sliders vary within and among populations, presumably depending upon both environmental and genetic factors. Usually, tropical and subtropical populations attain greater body size than those of temperate regions (Pritchard and Trebbau, 1984). Populations of particularly large individuals occur along the Caribbean drainage of Central America, with some females exceeding 400 mm in carapace length (Pritchard and Trebbau, 1984). D. Moll (pers. obs.) found 188 adult females in a northern Belize stream to have a mean plastron length of 292.2 mm (332 mm maximum) and 152 adult males to have a mean plastron length of 180.6 mm (301 mm maximum). Moll and Legler (1971) recorded the largest female in their Río Chagres study area at 352 mm carapace length (CL) and 345 mm plastron length (PL), and the largest male at 342 mm CL and 304 mm PL. Tropical South American subspecies do not seem to be as large. Pritchard and Trebbau (1984) measured 14 unsexed *P. s. chichiriviche* from a lake in Venezuela that ranged from 185 to 305 mm PL and 195 to 325 mm CL. The authors stated that this subspecies is larger than *P. s. callirostris*. Colombian females attaining 300 mm CL and males reaching 252 mm CL were reported by Medem (1975). Most females (190–240 mm CL) and males (150–200 mm CL) were smaller, however. Average adult size may have diminished because of overexploitation of adults for human consumption (Medem, 1975; Pritchard and Trebbau, 1984).

Growth cycles and possible factors influencing growth in Río Chagres sliders were studied by Moll and Legler (1971). Hatchlings begin to grow after reaching the water and beginning to eat. Growth is rapid in the years prior to sexual maturity, then slows markedly with age. Juvenile females and males grow at about the same rate until the third year, when most males approach sexual maturity and their growth slows markedly. Females continue to grow rapidly through their third and fourth years, but growth declines markedly by their fifth year as some reach maturity. Sexual maturity is attained by males around 125–135 mm PL in two to four years and by females around 240–260 mm PL in five to seven years. D. Moll (pers. obs.) found Belizean *P. scripta* males to mature at about 130 mm PL in three to four years, and females at 248 mm PL in six to seven years. Attainment of sexual maturity has a marked effect on growth rate and ultimate size in *P. scripta*, because males not only mature sooner but also remain smaller than females, on the average, throughout life. In the population studied by Moll and Legler (1971) only 1% of adult males exceeded 300 mm PL, whereas 32% of adult females were over that size. Only 18% of the males attained the minimum size at which females reached puberty (240 mm PL). Adult growth in both sexes was characteristically slow and irreg-

ular, with indications (from fusion of plastral scutes) that growth may begin to cease in females exceeding 300 mm PL. No evidence for growth cessation in males exists, and the largest male that Moll and Legler captured (304 mm PL) showed a narrow zone of new growth.

Even though air and water temperature, food supplies, and photoperiod were nearly constant throughout the year, Río Chagres sliders displayed cyclic growth (Moll and Legler, 1971). Some growth in juveniles occurred in all months but was slowest during the rainy season (August–November), increased in December, and was relatively rapid throughout the dry season and early wet season (January–July). Growth rings formed whenever growth slowed or stopped. Moll and Legler determined that this usually occurred during periods of heavy rain and flooding, when sliders probably became inactive and did not feed. Juvenile growth was directly correlated with amount of sunlight available on a daily basis. Most adults did not grow during periods of maximal reproductive activity, when energy may be diverted from shell growth to gametogenesis or searching for mates.

Although mean and maximum sizes attained in tropical slider populations are usually larger than those attained in temperate populations, overall patterns of growth are similar (Cagle, 1946, 1948a, 1950; Webb, 1961; Moll, 1977). Growth is very responsive to environmental phenomena such as water temperature and food supply (Cagle, 1946, 1948a, 1950; Webb, 1961; Gibbons, 1970b; Avalos, 1975; Moll, 1977), and growth rings are formed when growth temporarily ceases. Growth is cyclic in temperate populations (Cagle, 1950) even if activity is continuous, as in southern springs (Jackson, 1964). The obvious difference between temperate and tropical populations is that opportunities for growth cease entirely when winter's cold temperatures force temperate populations into hibernation, limiting the growing season to a relatively short period of the year for most populations.

### Food Habits of Tropical Sliders

Tropical sliders are opportunistic feeders, normally eating a combination of plant and animal foods, the exact composition of which is largely dictated by size and sex of the turtles, and the food sources available in the particular habitat. Tropical sliders are capable of surviving almost anywhere by feeding on almost anything. In prime habitat, aquatic plants are an important component of the diet. In the Río Chagres, plants—especially waterweed (*Elodea* sp.) and grass (*Paspalum* sp.)—composed 93% of the total volume of food consumed by adults (Moll and Legler, 1971). Animal food was present in the gut contents of nearly half of the adults (49%), but it composed only of 7% of total volume. Animal prey consisted mainly of insects, carrion fish, and gastropods, the latter possibly ingested largely as a calcium supplement for gravid females.

Juveniles were more carnivorous than adults, but animal food still composed only 19% of their total food volume. D. Moll (1986) found that *P. scripta venusta* females in a heavily vegetated stream of northern Belize were omnivorous, ingesting large amounts of grass (*Paspalum peniculatum*), but animal food, mainly insects, made up nearly 31% of their food volume. Adult males were more insectivorous than females but still ate large amounts of plant material. Juveniles were almost entirely insectivorous. Moll and Legler (1971) found that *P. scripta* changed principal dietary components opportunistically, depending on availability. Flexibility is demonstrated by the presence of a dense population in a small muddy pond in which organic mud (or perhaps blue-green algae on mud) was the major dietary component, followed by roots and leaves from grasses on the pond margins and minute amounts of animal matter (Moll and Legler, 1971). Pritchard and Trebbau (1984) considered Venezuelan *P. scripta* to be equally flexible and opportunistic in diet, with one population (*P. s. callirostris*) known to prey on swimming waterfowl, and another population (*P. s. chichiriviche*) developing a macrocephalic condition often associated with molluscivory. Other dietary analyses and fragmentary data available concerning tropical populations confirm that *P. scripta* is opportunistic and omnivorous over its entire range (Moll and Legler, 1971). This flexibility helps to explain why sliders are successful over such a wide diversity of environments and habitats within their range.

Feeding habits of temperate *P. scripta* populations have been relatively well studied and can be described as essentially identical to those described above for tropical populations (see Cahn, 1937; Cagle, 1950; Carr, 1952; Webb, 1961; Ernst and Barbour, 1972; Moll, 1977). All populations are omnivorous, relying heavily on plant material but taking animal material whenever available. Some populations exist in barren and polluted habitats where little food other than that which is blown or washed into the water is available (Minyard, 1947; Cagle, 1950; Moll, 1977). Cagle (1944b) reported that *P. scripta* will forage for terrestrial vegetation on land, returning to water to swallow. Temperate juvenile *P. scripta* are characteristically more carnivorous than adults in most populations, and ontogenetic shifts in degree of carnivory (toward greater herbivory) occur (Clark and Gibbons, 1969; Hart, 1983).

### Reproduction in Tropical Sliders

#### MATING BEHAVIOR

Moll and Legler (1971) observed attempts at copulation by sliders in August, September, and October in the Río Chagres and assumed that mating also occurred between January and June because of a progressive reduction in

sperm levels in the epididymides and lipid levels in the interstitial cells of the testes during this period. The similarity of the timing of the male reproductive cycle in Panama to that of temperate males, which have spring and fall mating peaks (Cagle, 1950), also suggests that peaks of breeding activity may be similar. Medem (1975) reported that Colombian *P. s. callirostris* mate from September through December. Copulation usually occurs in quiet deep water (Moll and Legler, 1971; Medem, 1975) and takes only two to three minutes to complete (Medem, 1975). Available evidence indicates little or no elaborate precopulatory behavior in tropical sliders in comparison with temperate populations (Rosado, 1967; Moll and Legler, 1971; Medem, 1975).

#### REPRODUCTIVE CYCLE OF MALES

Moll and Legler (1971) found that testes are smallest and lightest from early January through May and are largest and heaviest from early July through December in Panamanian *P. scripta*. Epididymides enlarge later than the testes and remain enlarged well after testicular regression. In Panama, seasonal changes in size of testes are associated with the male's spermatogenic cycle. Spermatogenesis begins in May, when spermatogonia begin to proliferate in the seminiferous tubules, and Sertoli cells become less numerous. In June, spermatogonia predominate, primary spermatocytes are present, and in some males secondary spermatocytes, spermatids, and a few metamorphosed sperm are already present. Spermiogenesis is under way in July, and all spermatogenic and spermiogenic stages are well represented. Spermatogenesis continues from August through November, filling the lumina of most tubules with mature sperm. The spermatogenic cycle is completed about a month earlier in smaller males (below 190 mm PL) than in larger males, which may continue producing sperm until early December. The germinal epithelium is inactive from January through May (the Panamanian dry season). The epididymides begin receiving sperm in August, receiving peak amounts by January. Although some sperm are present all year, they reach their lowest level in the epididymides in June and July, possibly because of expenditure during the spring mating season. The spermatogenic cycle of male *P. scripta* in Panama does not differ appreciably in detail or timing from that of North Temperate *P. scripta* and other North Temperate chelonians that have been studied (see Moll, 1979, for a summary of male cycles and other references). Data concerning the reproductive characteristics of South Temperate populations are too sparse for meaningful comparisons.

#### REPRODUCTIVE CYCLE OF FEMALES

Moll and Legler (1971) divided the ovarian cycle of tropical sliders into four phases: (1) follicular enlargement, (2)

ovulation and intrauterine period, (3) oviposition, and (4) a period of quiescence, during which the ovaries are small and follicular development is minimal. Follicular enlargement begins in late August and September (the latter half of the rainy season), and follicles reach ovulatory size in late November and December in the Río Chagres population. Follicular development is continuous until late May, with large follicles ovulating while the next-largest class of follicles enlarge and become preovulatory. Follicular activity and ovarian weights are greatest from early January through March. In April and May the size and number of enlarging follicles and ovarian weights decrease markedly. Ovulatory-sized follicles disappear by late April. The ovaries are quiescent from June through July, when activity and weights are minimal. Ovarian cycles of *P. scripta* in Mexico and elsewhere in Central America are similar to those described above for the Panamanian population, but ovulation and oviposition probably begin and end later in more northern latitudes (Moll and Legler, 1971). The timing of the ovarian cycle of tropical sliders does not greatly differ from that observed in North Temperate emydids (see Moll, 1979, for a summary of cycles and other references). The most conspicuous difference lies in the constraints imposed by the shorter activity period of temperate species, resulting in greater crowding of the steps in the cycle (Moll and Legler, 1971).

#### REPRODUCTIVE CHARACTERISTICS OF TROPICAL POPULATIONS

The reproductive patterns of the tropical slider populations that have been investigated are remarkably similar (Table 12.1). Populations in Panama, Colombia, Venezuela, Mexico, Nicaragua, and Belize produce multiple (up to 6) clutches of 5 to 30 small (in relation to female body size), oblong, leathery-shelled eggs in flask-shaped cavities dug in relatively open sites during an extended spring nesting season. The eggs take between two and three months to hatch. The nesting seasons in most populations correspond with the dry seasons in their respective habitats, and the hatchlings tend to emerge with the onset of the rainy seasons. In Colombian *P. s. callirostris* and Venezuelan *P. s. chichiriviche* there is some possibility of a secondary nesting season in August (Medem, 1975; Pritchard and Trebbau, 1984). Although the data upon which these generalizations are based are limited for many tropical populations (and there are no data at all for many populations), they support the conclusions of the more extensive studies of Moll and Legler (1971) in Panama and of Medem (1975) in Colombia. These studies suggest a common reproductive strategy for extant slider populations across the Neotropics that is similar to that of temperate, presumably ancestral slider populations and is drastically different from that of many other tropical turtle species.

Table 12.1. Reproductive data concerning tropical sliders (*Pseudemys scripta*)

Location/subspecies	Reference	Eggs per clutch	Clutches per year	Egg characteristics (sizes in mm)	Nest characteristics	Incubation period (days)	Nesting season
Pacific coast of Isthmus of Tehuantepec, Mexico/ <i>grayi</i>	4	16-18	--	Oblong, oval, 16 x 45	--	--	Mar.
Atlantic drainage, Chiapas/Mexico/ <i>venusta</i>	5	12-20	--	Elongate, ≈25 x 40	Communal, flask-shaped, ≈200 mm deep	--	Jan.-Apr.
Pacific drainage, Chiapas/ <i>grayi</i>	5	10-20	--	--	On beaches of rivers and lakes	≈90	Feb.-Apr.
Atlantic drainage, Chiapas/ <i>venusta</i>	8	5-21	1-3	--	--	--	Feb.-May
Corozal district, Belize/ <i>venusta</i>	7	8-20	2-3	Oblong, leathery, flexible, ≈28.0 x 41.0	Flask-shaped cavity in fields	--	Feb.-May
Lake Nicaragua, Nicaragua/subspecies unclear	2	$\bar{X}$ = 20 (15-25)	--	--	--	--	--
Río Chagres, Panama Canal Zone/subspecies unclear, possibly <i>venusta</i>	2	$\bar{X}$ = 17 (9-25)	1-6	Oblong, leathery, flexible, $\bar{X}$ = 42.2 x 28.8	Communal, sealed flask-shaped cavity	71-86	Dec.-May
Department of Chocó, Colombia/subspecies unclear, possibly <i>venusta</i>	1	12-24	--	--	--	--	--
Northwestern Venezuela and northern Colombia/ <i>callirostris</i>	3,6	9-30	2-3	Oblong, soft-shelled, flexible, 21 x 27 to 26 x 41	Flask-shaped, maximum dimensions (mm) = 180 deep x 110 wide at entrance x 130 wide at base	69-92	Colombia: Dec.-Apr., perhaps a second season in Aug. Venezuela: Apr.-June principal season.
Northern Venezuela/ <i>chichiriviche</i>	6	11-28	--	--	--	--	Uncertain

References: 1, Medem, 1962; 2, Moll and Legler, 1971; 3, Medem, 1975; 4, Sumichrast, in Smith and Smith, 1979; 5, Alvarez del Toro, 1982; 6, Pritchard and Trebbau, 1984; 7, D. Moll, pers. obs.; 8, see Chapter 13.

Temperate and tropical slider populations would be characterized as possessing Pattern I reproductive strategies (Moll, 1979). This is a primitive pattern in which large, multiple clutches of relatively small, soft-shelled eggs are produced during a well-defined nesting season. Nesting occurs in well-defined areas, and nests are carefully constructed and sealed. Several other large freshwater and marine tropical genera have also evolved toward Pattern I strategies (e.g., *Batagur*, *Chelonia*, *Dermochelys*, *Podocnemis*, *Trionyx*). Alternately, many other tropical species that are smaller, aquatic and semiaquatic to terrestrial, and often morphologically specialized (e.g., *Cuora*, *Cyclemys*, *Kinosternon*, *Rhinoclemmys*) have evolved toward Pattern II reproductive strategies (Moll, 1979). Pattern II strategies entail the production of small clutches of relatively large, hard-shelled eggs, acyclic or year-round reproduction, solitary nesting with no special nest area, and nests poorly constructed or not even attempted (Moll, 1979). Although both strategies are successful, as evi-

denced by their recurrence in extant populations, Moll (1979) and Moll and Legler (1971) considered Pattern II as an advanced trait evolving in conjunction with trends toward smaller size and increasing specialization, and associated with long-term tropical residency. Two very old members of the Neotropical fauna (i.e., present by early to mid-Pliocene), *Kinosternon leucostomum* and *Rhinoclemmys funerea* (Savage, 1966), were studied in detail by Moll and Legler (1971) to provide comparisons with tropical *P. scripta* in Panama (Table 12.2). The oldest tropical resident of the three, *K. leucostomum*, whose genus is a member of the Middle American Element of Savage (1966), has the most extreme reproductive Pattern II, and the emydid *R. funerea*, whose genus, like *Pseudemys*, is a member of the Old Northern Element (Savage, 1966) but probably a much earlier tropical immigrant, has a reproductive pattern nearly as extreme toward Pattern II as *K. leucostomum*. Panamanian *P. scripta*, already considered a recent immigrant based upon biogeographic evidence

Table 12.2. Comparison of life history of *Pseudemys scripta elegans* in the United States and three species of turtles in Panama

Characteristic	<i>Pseudemys scripta elegans</i> , United States	<i>Pseudemys scripta</i> , Panama	<i>Rhinoclemmys funerea</i> , Panama	<i>Kinosternon leucostomum</i> , Panama
Size at sexual maturity (PL in mm)	90-100, male; 150-195, female	125-135, male; 240-260, female	≈200, male; ≈200, female	≈100, male; ≈80, female
Male gonadal cycle	Spermatogenesis in late spring and summer; spermiogenesis in fall; germinal epithelium quiescent in winter	Spermatogenesis begins in May and June; spermiogenesis July-Dec.; germinal epithelium quiescent Jan.-May	Cyclic; periods of gonadal quiescence short; spermatogenesis July-early May	Cyclic; periods of gonadal quiescence short; spermatogenesis and spermiogenesis in most months
Female gonadal cycle	Follicles begin enlarging autumn (Aug.?); ovulation late Apr.-late July	Follicles begin enlarging in late Aug. or Sept., mature in Dec.; ovulation late Dec.-May	Beginning of cycle unknown; ovulation at least Apr.-Aug.; most specimens from Aug. in postreproductive state	Continuous as a population; some individuals ovulating each month
Mean size of eggs (mm)	Leathery, flexible, oblong; $\bar{X} = 36.2 \times 21.6$ (Ill.), $37.7 \times 22.6$ (La.)	Leathery, flexible, oblong; $\bar{X} = 42.2 \times 28.8$	Hard, brittle shell; oblong; $\bar{X} = 68 \times 35$	Hard, brittle shell; oblong; $\bar{X} = 37.1 \times 19.4$
Mean size of hatchlings (mm)	32.8 PL, 34.2 CL; $N = 7$	35.2 PL, 36.5 CL; $N = 42$	58.5 PL, 64.0 CL; $N = 3$	25.6 PL, 32.7 CL; $N = 3$
Eggs per clutch	4-18, $\bar{X} = 9$ (Ill.); 2-19, $\bar{X} = 7$ (La.)	9-25, $\bar{X} = 17$	1-6, $\bar{X} = 3$	1-2; 1 more common
Clutches per season	1-3	1-6	1-4	Multiple
Nest	Communal; sealed flask-shaped cavity in ground	Communal; sealed flask-shaped cavity in ground	Solitary; probably no nest; eggs laid at surface and covered with leaf litter	Solitary; shallow nest, or eggs laid at surface and covered with leaf litter
Incubation period	67-79 days (24°-30° C)	71-86 days (20°-33° C)	98-104 days (≈20°-35° C)	126-148 days (20°-33° C)
Food habits	Opportunistic; omnivorous to vegetarian; feeds chiefly in water	Opportunistic; herbivorous when aquatic plants are plentiful; feeds only in water	Opportunistic; chiefly herbivorous; feeds equally well in and out of water	Opportunistic; omnivorous (snails, insects, aquatic plants); probably feeds only in water
Growth cycle	Cyclic; May-Oct. (Ill.); Apr.-mid-Nov. (La.)	Cyclic; greatest Jan.-Aug.; least Aug.-Dec.	Cyclic, but periods of growth unknown	Cyclic, but periods of growth unknown

Source: Modified from Moll and Legler, 1971.

Abbreviations: CL, carapace length; PL, plastron length.

discussed by Savage (1966), is further implicated in this regard by the great contrast between its reproductive pattern and that of the old tropical residents above, and by the great similarity of its pattern with that of its close temperate relatives, such as *P. s. elegans* (Table 12.2). Although ecological data concerning tropical *Terrapene* are too sparse for meaningful comparison, comparisons are possible between tropical slider populations and some Old World tropical species.

Other than the emydine genera *Pseudemys* and *Terrapene*, all members of the family Emydidae inhabiting the tropics belong to the subfamily Batagurinae. Considering that the greatest diversity of batagurines occurs in the Old World tropics of the oriental region, it is likely that the area has been both a major and an ancient center of evolution for the group. Most genera found in this region today are restricted to the tropics or at least the subtropics. Presumably then, life history traits shared by the majority

of this group, including the Neotropical representatives of the genus *Rhinoclemmys*, can logically be considered adaptations to a tropical environment.

In regard to reproduction, those batagurines for which we have knowledge (*Batagur*, *Callagur*, *Cuora amboinensis*, *Cyclemys dentata*, *Geoemyda silvatica*, *Kachuga*, *Melanochelys trijuga*, *Rhinoclemmys funerea*, and *Siebenrockiella*) appear to have seasonal sexual cycles correlated with rainy and dry seasons. However, some *Rhinoclemmys* may lay eggs throughout the year (see Medem, 1962; Pritchard and Trebbau, 1984). Perhaps the most distinctive feature of their reproduction is their tendency to produce exceptionally large, oblong eggs. Largest are the eggs of *Orlitia borneensis*, which average 79 mm × 43 mm and weigh around 100 g each. Another distinctive feature of the eggs of most batagurine species (particularly forest-dwelling forms) is their thick, brittle shell. This shell effectively makes these eggs independent of the hydric environment

Table 12.3. Mean reproductive specifications of selected batagurine emydids and temperate and tropical populations of the emydid *Pseudemys scripta*

Species	Locality	N	CL (mm)	Body mass (kg)	Clutch		Egg length × width (mm)	EMI	RCM
					Size	Mass (g)			
<i>Batagur baska</i>	Malaysia	40	488	17.9	26	1,694	66 × 40	0.36	0.095
<i>Callagur borneoensis</i>	Malaysia	75	466	16.8	11	799	70 × 41	0.42	0.05
<i>Cuora amboinensis</i>	Malaysia	2	175	1.00	1	19.5	47 × 26	1.95	0.02
<i>Cyclemys dentata</i>	Malaysia	2	200	1.25	3	89.1	56 × 29	2.30	0.07
<i>Heosemys spinosa</i>	Malaysia	1	186	0.95	1	48.7	65 × 35	5.10	0.05
<i>Kachuga dhongoka</i>	India	2	420	7.27	23	809	57 × 36	0.52	0.11
<i>K. kachuga</i>	India	1	560	21.10	17	940	64 × 40	0.26	0.044
<i>K. tentoria</i>	India	8	225	1.56	6	126	49 × 27	1.38	0.08
<i>Melanochelys trijuga</i>	India	1	175	0.76	3	45	44 × 22	1.98	0.06
<i>Orlitia borneensis</i>	Malaysia	2	475	12.40	12	1,132	79 × 43	0.70	0.09
<i>Rhinoclemmys punctulata</i>	Panama	1	243	2.70	5	187	52 × 34	1.4	0.07
<i>Sieberroekiella crasscollis</i>	Malaysia	3	186	0.94	1.3	37	52 × 30	3.0	0.04
<i>Pseudemys scripta</i>	Central United States	16	225	1.20	12	116	36 × 22	0.95	0.11
	Panama	8	333	4.20	20	421	43 × 28	0.49	0.10

Abbreviations: CL, carapace length; EMI, egg mass index; RCM, relative clutch mass.

(M. Packard et al., 1982) and hence possibly adapted to the high moisture content of tropical forest soils. With desiccation-resistant eggs, at least some batagurines have been able to abandon the traditional behavior of digging nests in the root-ridden, often waterlogged soils of the tropical forest in favor of placing their clutches in leaf litter and other protected sites at the surface (e.g., certain *Rhinoclemmys*; see Medem, 1962, and Pritchard and Trebbau, 1984). Eggs with brittle shells are probably also adaptive in repelling attacks by the profusion of ants and microbes inhabiting moist tropical forests. In support of this hypothesis, it is significant that the only batagurines known to lack brittle-shelled eggs are riverine species (*Batagur*, *Callagur*, and *Kachuga*), which typically nest on exposed sandbanks.

Table 12.3 summarizes reproductive characteristics of a selection of Malaysian and Indian batagurines. Clutch size varies widely within the group, but 1 to 3 large eggs are common for the smaller species, whereas clutches exceeding 20 eggs are found only in a few large riverine forms such as *Batagur* and *Kachuga dhongoka*. Body size is not necessarily a good predictor of clutch size in batagurines, because certain large species such as *Orlitia*, *Callagur*, and *Kachuga kachuga* lay relatively small clutches.

Although a thorough examination of batagurine reproductive strategies is impossible because of a lack of ecological data on most species, a general comparison of the reproductive output of certain species is possible and provides some insight into how batagurines have adapted to the tropical environment. Two instructive statistics are egg mass index (EMI) and relative clutch mass (RCM). EMI and RCM respectively measure the size of the egg and the size of the clutch relative to the body size of the female turtle. EMI is the weight of the egg divided by the

weight of the spent female multiplied by 100. RCM, modified from the usage of Vitt and Price (1982), is the clutch mass divided by the body mass of the spent female.

Relative to their body size, small turtles put a proportionately greater investment into each egg than do large turtles. Consequently the EMI is negatively correlated with the size of the female. Figure 12.1 shows the regression of a logarithmic plot of the EMIs on carapace length for the 12 tropical and subtropical batagurine species listed in Table 12.3. The mean EMI for 16 sliders from the central United States (solid circle) and for 8 Panamanian sliders (open circle) are shown. This graph supports the idea that the temperate-adapted sliders put a much lower energy investment into individual eggs than do comparably sized batagurines (both slider plots fall below the 95% confidence limits of the regression line). Tropical sliders show no convergence toward the batagurine condition. In fact, a line drawn between the EMI plots of temperate and tropical populations parallels the batagurine line, suggesting that the EMI-body size relationship is the same in batagurines and emydines.

The RCM presents a more confusing picture. Small batagurines (less than 30 cm CL) have low RCMs (0.02 to 0.08). The larger species show a dichotomy, with *Batagur*, *Kachuga dhongoka*, and *Orlitia* having high RCMs (greater than 0.09), whereas *Callagur* and *Kachuga kachuga* have relatively low RCMs (0.05 or less). These large differences in RCM, at least between *Batagur* and *Callagur*, may be related to a higher degree of density-independent mortality in the former (E. Moll, 1986a). Despite rather large differences in the EMI, the temperate and tropical slider populations used for comparison do not differ significantly with respect to RCM (0.11 and 0.10). Relative to batagurines of comparable body size, the slider popula-



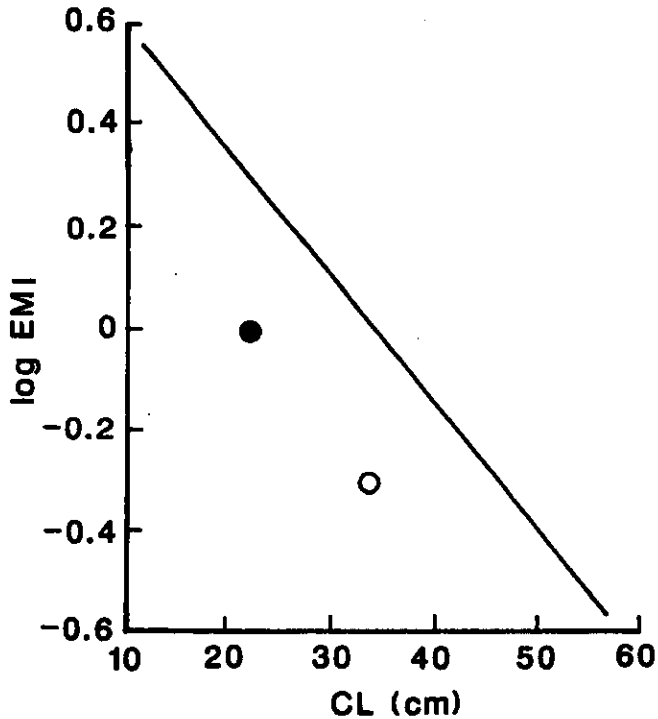


FIGURE 12.1. Regression of egg mass index (EMI) on carapace length (CL) in 12 tropical and subtropical batagurine emydids. The solid circle represents the EMI of 16 sliders from central Illinois; the open circle, the EMI of 8 Panamanian sliders. The regression line is calculated by this formula:  $\log \text{EMI} = 0.8506 - 0.02524(\text{CL in cm})$ .

tions have larger RCMs. From these data, one could conclude that *Pseudemys* expend less energy on individual eggs but put more into a clutch than do the batagurines. However, this conclusion is negated by other studies among sliders; for example, populations studied by Congdon and Gibbons (1985) in South Carolina have a mean RCM of only 0.05. The factors causing the aforementioned interspecific and intraspecific variability in the RCM are in obvious need of study. The RCM may be more useful in studying adaptation of species and populations to more-localized environmental conditions than as a generalized adaptation to the tropical environment.

Moll and Legler (1971) found that clutch size in Panamanian *P. scripta* was positively correlated with increasing body size (plastron length) of gravid females. Cagle (1950) reported a similar correlation in *P. s. elegans*, and Gibbons et al. (1982) and Congdon and Gibbons (1983, 1985) demonstrated a similar relationship in *P. s. scripta*. Emphasis on accumulating mensural data rather than weights in the study by Moll and Legler (1971) precludes detailed comparisons concerning some relationships between female body size and egg-clutch components discovered by Gibbons et al. (1982) and Congdon and Gibbons (1983, 1985) in temperate *P. s. scripta* (see comparisons of

RCM above, however). They found that in addition to clutch size and egg width, clutch wet mass and egg wet mass increased with female body mass and length. Congdon and Gibbons (1983, 1985) also determined that mean egg width in *P. s. scripta* is probably a better indicator of reproductive output than is egg length (used by Moll and Legler, 1971) in determining parental energy investment per egg as clutch sizes increase. Therefore, the observation by Moll and Legler (1971) that mean egg length decreases as clutch size increases may not indicate less parental investment per egg with increasing clutch size in tropical populations. Congdon and Gibbons (1985) found no direct evidence for a trade-off between egg size and clutch size in temperate *P. s. scripta* populations. Also, because no long-term studies of marked populations have been conducted in the tropics, other comparisons with temperate *P. scripta* concerning variation in annual clutch size or clutch frequency are not possible at this time.

The most apparent difference in the life histories of Neotropical sliders, as compared with temperate populations, lies in their increased reproductive potentials, which, as stated above, are directly related to larger body sizes attained in most tropical populations (see Tables 12.1 and 12.2; Cagle, 1950; Moll and Legler, 1971; Gibbons, 1982; Gibbons et al., 1982; Congdon and Gibbons, 1983, 1985). High reproductive potentials may be necessary for survival of Pattern I species in tropical habitats because of the intensity of predation on eggs and young (Moll and Legler, 1971; Medem, 1975; Drummond, 1983). Greater reproductive potentials and larger size are probably directly related to the extended annual activity period permitted by tropical climates. Feeding can continue throughout the year, and although growth rates, as discussed, are largely cyclic, some growth in individuals in the population may occur throughout the year (Moll and Legler, 1971). Another selective force favoring large size in some tropical populations may be predation by crocodilians, because crocodilians and sliders are sympatric over much of the latter's tropical range. Although reproduction is also cyclic, the benign climate allows a much longer nesting season than is possible in temperate zones (Moll and Legler, 1971), consequently allowing more clutches to be successfully oviposited in a given season. The increased reproductive potentials in tropical populations are approximated (to a lesser extent) in temperate populations of *P. scripta* from heated impoundments (Gibbons, 1970b; Thornhill, 1982), probably through a similar interrelationship of temperature, primary productivity, feeding, and growth phenomena.

These data suggest only differences in degree rather than drastic changes in the reproductive ecologies of slider tropical populations when compared with temperate populations. Even the characteristic of nesting during the dry season is not clearly a tropical adaptation, because North

Temperate populations would presumably ovulate and oviposit at the same time of year if the reproductive cycle were not interrupted by a period of hibernation in winter (Moll and Legler, 1971). The cycle of dry-season nesting and wet-season hatching (characteristic of many tropical reptiles) may be a fortuitous result of a temperature-induced temperate gonadal cycle preadapted to fit into it.

### Conclusions

Moll and Legler (1971) concluded that the Neotropical slider is a tropical turtle by virtue of its distribution, not its ecology. It is morphologically and ecologically closer to North Temperate subspecies of *P. scripta* than it is to any tropical turtle. In the 18 years that have elapsed since that study was published, additional data on tropical slider populations from different locations have supported this conclusion.

*Pseudemys* presumably evolved into a generalist and an opportunist in the Holarctic region. These traits, which were so suited to the unpredictable temperate environment, also preadapted *P. scripta* for dispersal into the Neotropics during the subsequent environmental and geological turmoil of the Pleistocene. A plausible scenario is that the slider invaded and moved through the tropics to emerge in the South Temperate Zone during a period or periods of drought and lowering of sea level, which brought about recession of the rain forest and created corridors along the coasts. With no other large, diurnal, basking, predominantly aquatic emydids with which to contend, sliders flourished and spread in the new environment. With the return of pluvial conditions, however, the rain forest (perhaps with rain-forest-adapted turtles such as the pelomedusids) reinvaded much of its former range, thus fragmenting the sliders' range (e.g., eliminating it from the Amazon Basin). The success of another generalized tropical invader, *Homo sapiens*, may have prevented extirpation of sliders in some parts of the tropics by maintaining clearings in the reinvading forest.

Today, despite extreme differences in environment, the life history of tropical sliders is still similar to that of their temperate zone ancestors. The most significant differences in the ecologies of temperate and tropical slider populations are related to reproduction. In particular, the nesting season is longer, reproductive potential is greater, and eggs are larger in the tropical turtles. For the most part these differences can probably be attributed to direct environmental effects of the year-round warmth of the tropical climate, not to major genetic changes. Nesting seasons can begin earlier in the year and last longer than in temperate habitats. Tropical sliders feed and grow throughout the year, although rates may vary with the season. They may grow to larger size in this environment,

and egg size, clutch size, and perhaps number of clutches in turn are related to the body size of the female.

Batagurine emydids have evolved in the Old World tropics and today are largely confined to tropical and subtropical environments. The majority of these tend toward Pattern II reproduction, laying small clutches of exceptionally large eggs. Sliders, temperate and tropical, are typical of the majority of emydines, which lay moderate to large clutches of relatively small eggs (tending toward Pattern I reproduction). There is no indication that tropical sliders have been evolving in the direction taken by the batagurines, their closest aquatic and semiaquatic tropical relatives.

A final question to be explored concerns why tropical slider populations have not adapted appreciably to this new and radically different environment. Moll and Legler (1971) offered the explanation that lack of adaptation was due to the relatively recent arrival of the species into the tropics, suggesting that time had simply been insufficient for new adaptations to evolve. In light of recent evolutionary theory, however, it is conceivable that *Pseudemys scripta* will never change appreciably, no matter how long it remains in the tropics. The publication of the punctuated equilibrium concept by Eldredge and Gould (1972) has offered an alternative view of how organisms adapt to their environments. It is their thesis that species to a large extent maintain their adaptations for long periods without change. They contend that most changes in adaptation are associated with speciation events and that once adaptation is established, little change occurs thereafter.

Species are often viewed as being tied to particular habitats. Rather than adapting to new habitats as environmental conditions change, most species track (i.e., follow) their old habitat. Where new conditions prevail, open niches may be filled by speciation events or by species preadapted to these new conditions (a process called species selection; see Eldredge, 1985, for review). Generalist species such as the slider are best able to track favorable habitat conditions in changing environments. Because of their generalized nature, they can occupy a wider geographic range and will likely persist longer as species than specialist types will. This view, which has gained considerable credence since being proposed in 1972, predicts that we might expect the generalized slider turtle to have a promising future in the tropical environment. Furthermore, as man continues to alter the tropical environment through clearing of the forest, slider turtles may be among the few species to benefit.

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