

Reproduction and Growth

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Turtle Eggs: Their Ecology and Evolution

Abstract

The state of knowledge about eggs of the slider turtle is presented, based on a general review of the literature and on data acquired in studies in South Carolina. Features of turtle eggs that appear critical to understanding how they protect and fuel the embryo are discussed. These include determination of the amount of energy a female dedicates to each egg and to the entire clutch and determination of the time over which energy is harvested, stored, and allocated. The importance of nest site selection by females and the environmental factors of soil moisture, texture, and temperature is discussed. Consideration is also given to the composition of the shells, yolk, and albumen of eggs in the context of protecting and fueling the developing embryo and hatchling. Ideas that are considered critical to understanding the evolution and current function of turtle eggs are discussed, and key questions that must be answered are presented.

Introduction

Many of the divergences in the natural and life histories of present-day amphibians and reptiles can be traced to the differences in their eggs. Primitive reptiles, the romeriid captorhinomorphs, apparently produced a relatively naked amniotic egg similar to the eggs of present-day amphibians that develop in terrestrial nests and produce a miniature adult rather than a larval stage (Carroll, 1969). The latter similarity suggests that, compared with aquatic amphibians, primitive reptiles had a longer developmental time within the egg and required greater amounts of egg yolk to provide the material and energy reserves to support the developing embryo until it hatched from the egg, and possibly for some time after. Reptile eggs have since developed a shell that helps to shield the egg's contents from its environment.

The eggshells of present-day reptiles may have evolved to protect the egg's contents from desiccation, bacteria,

fungi, and arthropod predators (Gray, 1928; Needham, 1931; Carroll, 1969; Packard and Packard, 1980). Eggshells of contemporary reptiles exhibit a wide range in type, texture, and configuration (Agassiz, 1857; Giersberg, 1922; Erben, 1970; Packard et al., 1977; Ewert, 1979; Packard and Packard, 1979; Sexton et al., 1979; Packard, 1980; Ferguson, 1982, 1985; Lamb and Congdon, 1985; Allison and Greer, 1986; Packard and Hirsch, 1986). Two major features of reptile eggs separate them from those of aquatic amphibians: (1) a much larger proportion of yolk and (2) a highly developed calcareous shell. These features combine to make the eggs of reptiles more resistant to desiccation and better able to fuel a longer developmental period and provide nutritional support for the hatchling after it leaves the egg.

In contrast to both lizards and snakes, there are no known viviparous turtles, nor are any turtles known to routinely delay laying eggs after they have been ovulated. Therefore, the shelled egg represents, in essence, the first environment that every turtle embryo is exposed to, and that environment is soon totally independent of the parent. The eggshell's role of protecting the embryo, a vulnerable stage in a turtle's life history, may thus be partially analogous to the role played by the carapace and plastron of adult turtles. Turtle eggs must provide all aspects of an embryo's needs from the time the eggs are independent of the female until the hatchling leaves the nest, a period that may exceed one year (Goode and Russell, 1968; Gibbons and Nelson, 1978). In addition, recent investigations indicate that the egg acts as a container of material for preovulatory parental investment in care (Kraemer and Bennett, 1981; Congdon et al., 1983a,c; Congdon and Gibbons, 1985; Wilhoft, 1986). The amount of preovulatory parental investment in care is not trivial. At least 50% of the contents of a turtle egg may remain in the form of hatchling fat bodies or residual material in the yolk sac. The residual yolk provides material and energy for maintenance, and possibly growth, of hatchlings after they leave the egg. Thus, the attributes of turtle eggs, and indeed all reptilian eggs, make them excellent subjects for examining the concepts of parental investment and optimal egg size.

The purposes of this chapter are (1) to place our knowledge of the eggs of *Trachemys scripta* in relation to knowledge about other turtle eggs, (2) to review and consolidate information about turtle eggs, (3) to identify the features that seem critical to our understanding of how turtle eggs protect and provide for their embryos in various nest environments, (4) to review and develop ideas that will increase our understanding of the evolution and present function of turtle eggs, and (5) identify areas in which our knowledge of turtle eggs is lacking and to pose important questions that remain to be answered. Progress toward these goals will require a review of material on egg components and developmental processes related to hatchling

viability and quality. In addition, it will require consideration not only of the egg itself but also of the timing and variation of investment in eggs; the nesting behavior of females related to nest site selection, the range of variation in the microenvironments within and among nests, and how environmental variation affects the survivorship of eggs and hatchlings; and the relationship between levels of preovulatory parental investment and survivorship of hatchlings. This chapter will not attempt to review all that is known about egg sizes or developmental stages of embryos. For viewpoints on other aspects of reptilian egg biology, see the following reviews and key papers: embryo development (Agassiz, 1857; Rathke, 1848); turtle eggs (Ewert, 1979, 1985; Miller, 1985); eggs, reproduction, and life histories of turtles (Wilbur and Morin, 1988); physiological ecology (Packard et al., 1977); evolution of the cleidoic egg (Packard et al., 1980); function of crocodilian eggs (Webb et al., 1987); crocodile egg chemistry (Manolis et al., 1987); the adaptive value of lipids in biological systems (Hadley, 1985); and lipid analysis (Christie, 1982).

Development of Eggs

The amount of energy available for production of eggs can come from resources harvested and sequestered during the period that the eggs are being produced or from energy and material stored previously. To understand reproduction in turtles, it is necessary to know the total amount of energy allocated to each clutch of eggs, the amount allocated to each egg, the time over which the energy was harvested and allocated, and the relative contributions of stored versus directly harvested energy for each clutch.

In *Chrysemys picta*, follicle sizes are smallest in the ovaries just after the nesting season, with substantial follicle enlargement taking place from late August through October (Ernst, 1971d; Congdon and Tinkle, 1982b). On average, the set of largest follicles found in females in October represented 50% of the energy of a complete clutch of eggs that would be laid during May and June of the following year. Energy allocated to follicle enlargement during the summer and early fall months was presumably obtained directly from harvested resources because stored lipids in females also increased during this period. The additional 50% of the energy to complete follicle enlargement prior to ovulation was allocated between spring emergence in late-March through mid-May when nests for first clutches were initiated (Congdon and Tinkle, 1982b).

The energy allocated to follicles during spring presumably came entirely from stored body lipids because the decrease in lipid levels of females during the period was almost equivalent to the increase in lipids in follicles (Congdon and Tinkle, 1982b). In addition, examination of growth in *C. picta* from Michigan and Pennsylvania indicated that little or no growth, and presumably feeding

activity, was taking place before June (Sexton, 1959a, 1965; Ernst, 1971a). A similar pattern of follicle development during late summer has been observed in *Sternotherus odoratus* in Alabama, where follicles were fully developed (ovulatory size) between August and December, with ovulation occurring during late April of the following year (McPherson and Marion, 1981a).

The minimum interval between the first and second clutches of *C. picta* in Michigan and *T. scripta* in South Carolina is approximately 12 days (Gibbons and Greene, unpub. data). This short interval indicates that (1) ovulation of a subsequent clutch of eggs can occur shortly after a clutch has been placed in a nest and (2) the follicles for the second clutch develop at the same time as those for the first clutch and, if necessary, complete development during the time the eggs for the first clutch are in the oviducts. In species in northern latitudes, energy for the second clutch probably comes primarily from stored lipids, because feeding activity would still be minimal during the period of egg development. In turtles from more southern latitudes, such as *T. scripta*, proportionally more energy in subsequent clutches may come directly from harvested energy rather than stored reserves; however, the relative contributions of the energy sources have not been documented.

Turtle Nests and Nest Site Selection by Females

Nests of many, and probably most, freshwater turtles are placed in areas that are exposed to full sunlight during some portion of the day. Nests are usually constructed in sandy to loam soils with little vegetation cover. Disturbed areas such as road banks, railroad grades, dikes, levees, and dams seem to be favored for nesting (Burger, 1977; Obbard and Brooks, 1980, 1981a; Petokas and Alexander, 1980; Seigel, 1980a; Snow, 1982; Congdon et al., 1983b, 1986; Obbard, 1983; Schwarzkopf and Brooks, 1987). Freshwater turtles generally dig flask-shaped nests in well-drained soils with their hind feet. Both within and among species the size of the nest and the number of eggs placed in the nest are in general positively related to the body size of the female (Congdon and Gibbons, 1985). Some turtles such as *S. odoratus* may deposit their eggs in muskrat mounds (Carr, 1952) or rotting stumps of trees but in some instances may only partially bury them or leave them entirely exposed (Risley, 1933; Ewert, 1979). Some species of the genus *Rhinoclemmys* cover their eggs with leaves (Medem, 1962; Moll and Legler, 1971). It seems logical that eggs in poorly covered nests will most often be in habitats that are shadier and more moist than the sites of covered nests, and in most if not all cases the eggs should have relatively impermeable rigid shells.

Temperature and soil moisture are major variables in the nest microenvironment and have been shown to be important in determining the ultimate survivorship and quality as well as the sex of developing embryos (Pieau, 1972,

1982; Bull, 1980, 1983; Bull and Vogt, 1981; Mrosovsky, 1982; Caudle, 1984; Packard et al., 1985; Congdon et al., 1987). Both of these factors, in conjunction with the number and possibly the size of eggs in a nest, have been shown to influence the rate of development and total incubation time before emergence from the egg. However, arguments that larger eggs of the terrestrial box turtle, *Terrapene carolina*, represent an adaptation for incubation and egg development in terrestrial environments (Packard et al., 1985) are not logical, because the eggs of most aquatic species also incubate and develop in terrestrial situations.

We suggest that the following scenario, modified from Wilbur and Morin (1988), is more likely. The relatively larger eggs of terrestrial turtles, compared with those of aquatic species with similar body size, may result from the requirements of hatchlings after they leave the nest. Hatchlings of aquatic species move to highly productive habitats containing high densities of aquatic insect adults and larvae. Thus, in such habitats hatchlings can attain a positive energy balance in a relatively short time. We do not agree with Wilbur and Morin (1988) that the speed and maneuverability of aquatic hatchlings, relative to terrestrial hatchlings, play a major role in their ability to attain a positive energy balance. In contrast to the productive environment encountered by hatchlings of aquatic turtles, hatchlings of terrestrial species emerge into an environment in which the distribution of prey is less dense and probably more clumped. These factors probably result in terrestrial turtles' being more herbivorous and less able to attain a positive energy balance in as short a time as do aquatic hatchlings. Thus, we propose that for terrestrial turtles (1) larger energy stores are provided by the parent and result in larger eggs and possibly larger hatchlings, (2) the ability to make longer movements among resource patches is enhanced by larger body size, and (3) a slightly larger body size may be necessary for increased gut length and volume related to herbivory.

A third feature of the nest environment that is less studied but may also be important is gas exchange between the embryos and the nest's surroundings. To what degree the female can ascertain the present conditions of the nest site or predict the future nest microenvironment to which her eggs will be exposed is not known but is certainly important to our understanding of turtle reproduction.

Both the depth of a nest and the egg's position within a nest determine the microenvironment of each egg. Eggs in shallow nests or at the top of nests would be expected to be exposed to larger diel and longer-term temperature variations than those deeper in the soil (Figs. 8.1 and 8.2). For example, temperatures at the surface of the soil exposed to full sunlight in South Carolina during late summer can reach daytime highs of more than 40° C, whereas those at 10 to 15 mm below the surface might not reach 35° C.

The lower thermal limit for turtle eggs incubated at relatively constant temperatures is approximately 22° C.

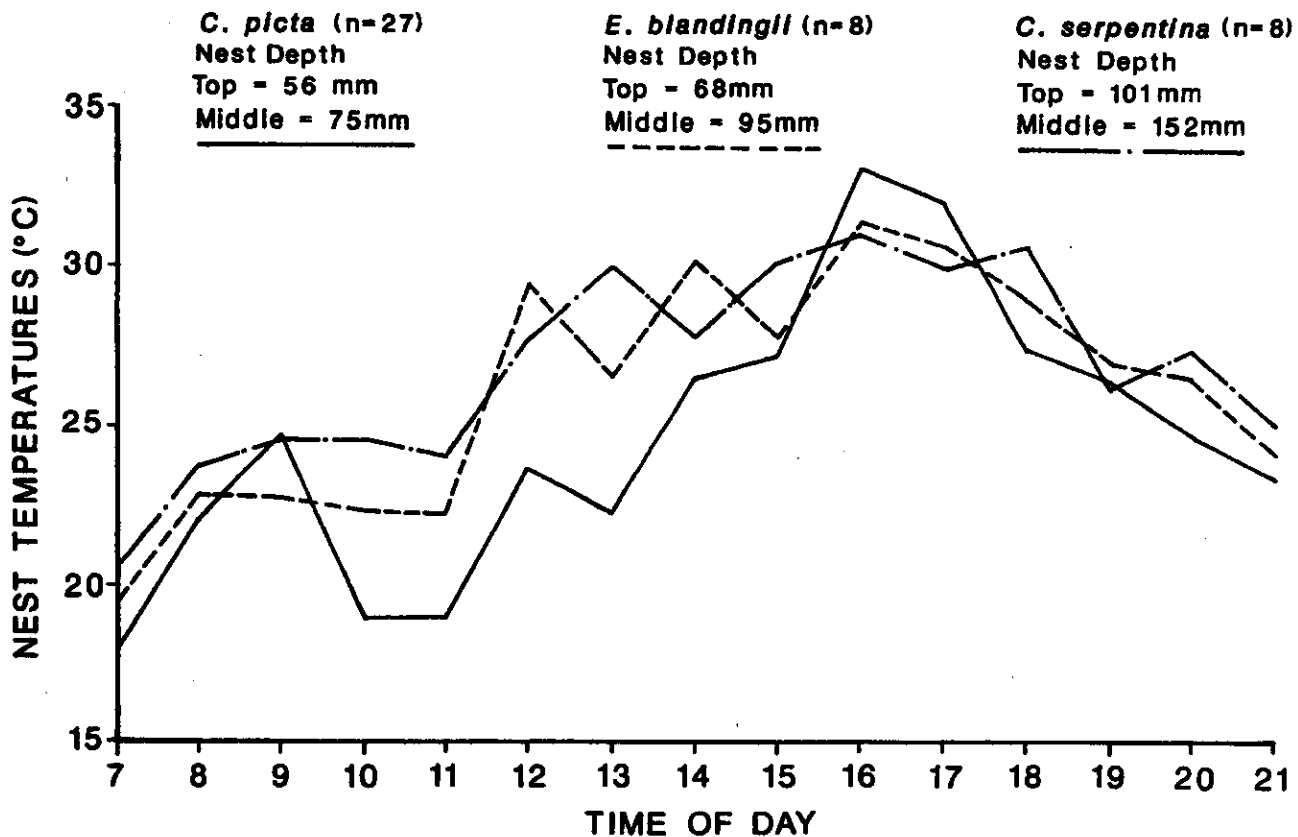


FIGURE 8.1. Average hourly temperatures over the entire incubation period taken from the center of nests of three species of turtles on the E. S. George Reserve in southeastern Michigan.

Below this temperature turtles such as *Chelonia mydas* (Bustard and Greenham, 1968; Bustard, 1971), *Chelydra serpentina* (Ewert, 1979), and *Chrysemys picta* (Ream, 1967) failed to develop. Minimum incubation temperature for turtles of the genus *Trionyx* may be closer to 25° C (Ewert, 1979). The thermal maximum above which turtle embryos cease development and die appears to be approximately 33° C (Yntema, 1960; Ewert, 1979). However, turtle embryos are certainly able to withstand short periods with temperatures below and above these thermal limits. Nest temperatures below the lower extremes may be common during the early portion of nesting seasons, but with the exception of very shallow nests, it is difficult to envision conditions in which eggs would be commonly exposed to temperatures above the upper lethal limits (Fig. 8.1).

Composition and Function of Eggshells

Eggshells of contemporary turtles are composed of two membranes of dense fibrous material that is thicker than that found in bird eggs (Schmidt, 1943; Young, 1950; Packard and Packard, 1979). The inner shell membrane lies next to the albumen, and the outer shell membrane lies next to the inorganic crystalline layer (Fig. 8.3). The

membranes are so closely apposed that they cannot be visually distinguished except at the white patch, or air cell, that forms between them at the top of the egg (Einem, 1956; Ewert, 1979; Packard and Packard, 1979). The eggshell and membranes associated with the air cell contain 26% less water than do the membranes from translucent areas of the egg (Thompson, 1985). Thus, the air cell is apparently an area of regional drying that is related to gas exchange required by respiration of the developing embryo (Thompson, 1985).

The inorganic portion of eggshells of both fossil and contemporary turtles is composed primarily of calcium carbonate (CaCO_3) in the form of aragonite (orthorhombic CaCO_3). The eggs of most other squamates and birds are calcite (Erben, 1970; Erben and Newesley, 1972; Solomon and Baird, 1976; Ferguson, 1982, 1985; M. Packard et al., 1982; Hirsch, 1983). Variation in the relative amounts of calcite and aragonite reported for eggshells of captive sea turtles (*Chelonia mydas*—Solomon and Baird, 1976) and pythons (Solomon and Reid, 1983) indicates that (1) reptiles may alter the type of crystals formed in their eggshells in response to conditions that exist in farms or zoos, and (2) reptiles have some physiological capability of producing the crystal type that is atypical for their group. These two factors suggest that if there is a function-

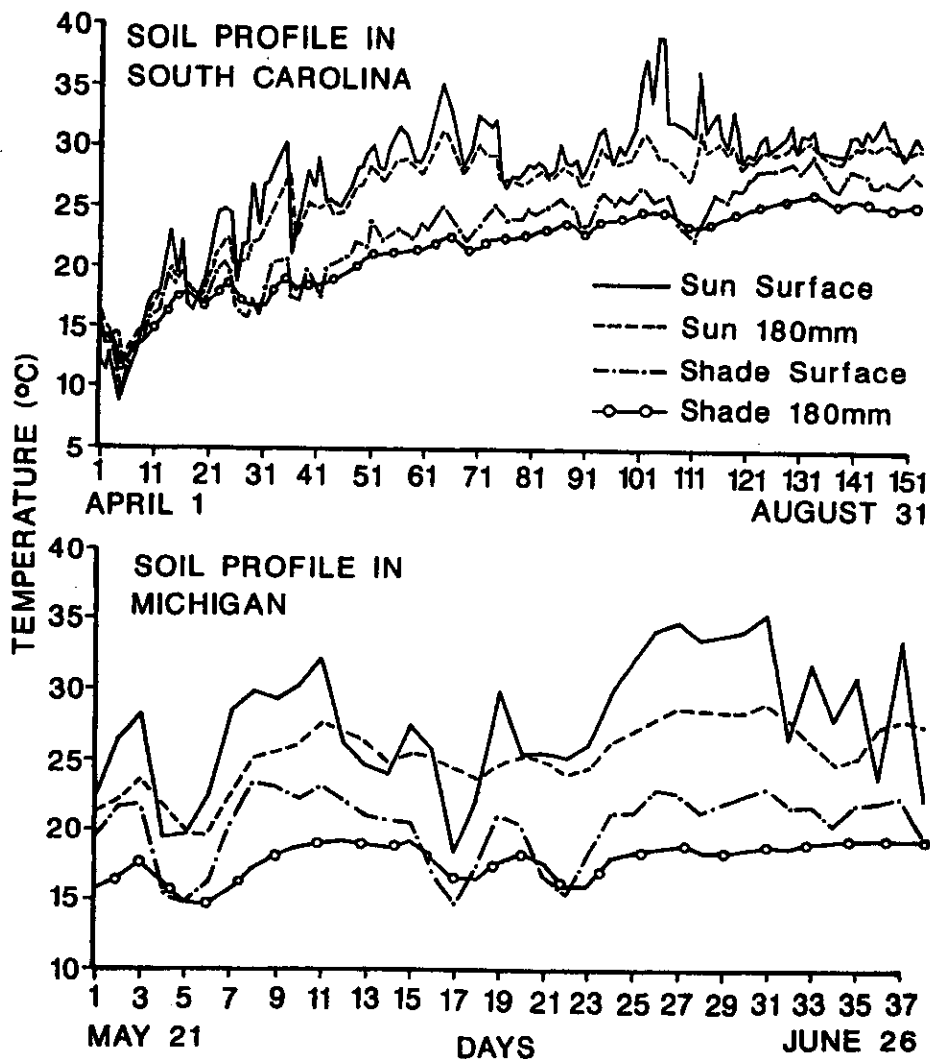


FIGURE 8.2. Soil temperature profiles in full sun and shade from the Savannah River Plant in South Carolina and the E. S. George Reserve in Michigan.

al difference in the type of eggshell crystals, natural selection could act upon variability in the trait.

Among the amniote eggs of contemporary reptiles, there are three main types of eggshells, based on the degree of calcification: (1) parchmentlike—a shell with little or no calcareous material (found in snakes and lizards), (2) flexible calcareous—a shell that ranges from a weakly defined calcareous layer to a discrete calcareous layer of loosely arranged shell units that do not interlock, and (3) rigid—a shell that has a thick calcareous layer with well-defined shell units that interlock. As a general rule, shell units of flexible eggshells are wider than tall and have distinct pores that penetrate to the underlying shell membranes, whereas shell units of rigid eggshells are taller than wide and have pores that are less structured than those of flexible-shelled eggs. Modern turtles have flexible calcareous or rigid eggshells (Ewert, 1979). Carettochelyids, chelids, dermatemydids, kinosternids, testudinids, and trionychids produce rigid-shelled eggs, and cheloniids, chelydrids, and dermochelyids produce flexible-shelled

ones. Within the emydids and pelomedusids, eggshell type varies among species (Ewert, 1979, 1985; M. Packard et al., 1982).

Eggshells of six species of emydid turtles with flexible-shelled eggs ranged from 15.8% to 20.6% ($\bar{x} = 19.2\%$) of the total dry mass of the eggs, with eggshells of *Trachemys scripta* averaging 18.6% (Congdon and Gibbons, 1985). Eggshells of *Clemmys marmorata*, an emydid turtle with brittle-shelled eggs, averaged 39.6% of the total dry mass of eggs. Five turtle species with brittle-shelled eggs had eggshells that averaged 40.8% of the total dry mass of eggs. The proportion of total egg dry mass in eggshells of the two eggshell categories was significantly different (Congdon and Gibbons, 1985).

The total amount of inorganic material found in the flexible eggshells of four species of turtles ranged from 35.9% to 39.3% and averaged 38.0% by dry mass (Lamb and Congdon, 1985). Eggshells of *T. scripta* averaged 39.3% inorganic ash by dry mass, and the inorganic ash in the shell averaged 7.4% of the total dry mass of the egg.

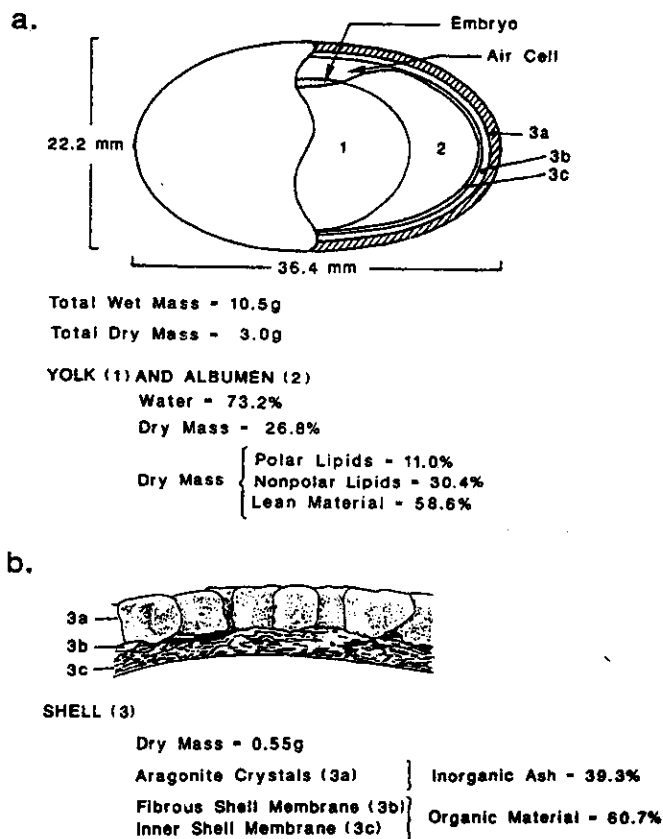


FIGURE 8.3. Schematic diagram of a typical *Trachemys scripta* egg.

Among five species with rigid eggshells, inorganic material ranged from 50.4% to 52.9% and averaged 51.8% by dry mass. The inorganic portion (approximately 22%) of the eggshell of the sea turtle *Chelonia mydas* (Solomon and Baird, 1976) was notably lower than the portions reported above for freshwater and terrestrial turtles. Whether the low inorganic level is normal for sea turtles is difficult to say at this time, because eggshells of sea turtles represent a distinct subgroup of flexible-shelled eggs in which (1) the shell units are smaller and less distinct, (2) the crystallites of aragonite are larger and more variable in size, and (3) the pores are not distinct, but numerous spaces penetrate the inorganic layer (Baird and Solomon, 1979; M. Packard et al., 1982; Hirsch, 1983). Also, the turtles were raised in captivity, which may have influenced the amount of inorganic content in their eggshells and the type of the calcium carbonate crystals formed as well (see the discussion of eggshell crystals above).

The reason that turtles are the only group of reptiles that produce eggshells made from aragonite rather than calcite crystals is unknown. It may be that the use of aragonite crystals is a primitive trait that arose early in the evolution of turtles. In contrast, the different eggshell

types found among turtles may be the result of selection pressures that are associated with different nest microenvironments, although ecological correlates of eggshell types with present-day nest environments have not been identified and are not readily apparent. For example, eggs of some crocodylians are placed in nests in sandy soils or in nests constructed of decaying vegetation. Similar substrates can be found in turtle nests, and indeed some turtles lay their eggs in alligator nest mounds (Deitz and Jackson, 1979; Kushlan, 1980). Regardless of crystal or eggshell type, it is apparent that the shells of reptile eggs protect the egg's initial contents and the developing embryo from a range of biotic and abiotic dangers.

Egg Component Studies and Data Reporting

Comparisons of egg or body components among studies are sometimes confounded by the lack of uniform techniques for determining the amounts of materials that make up the egg. In addition, there is a lack of uniform reporting of actual values and the way that proportions of egg components are expressed. Some of these differences result because the types of questions being asked vary, and different techniques will remain in use. However, some of the problems could be avoided with a few basic rules for extracting lipids and for reporting data. We will attempt to standardize the reporting of certain data from egg component studies.

Two general classes of lipids exist that differ in their solubility in organic solvents. Polar lipids are combinations of nonpolar fatty acid chains associated with a polar functional group such as phosphate or sugars. Polar lipids are generally extractable in a highly polar solvent such as methanol, ethanol, or chloroform (Christie, 1973). Nonpolar lipids such as triglycerides or cholesteryl esters are soluble in a less polar solvent such as ether, hexane, benzene, or cyclohexane but may also be extracted in a slightly more polar solvent such as chloroform or diethyl ether (Christie, 1973).

The choice of extraction technique should be made based on the questions asked. Polar lipids are usually associated with cell membranes and other structural components of animals such as myelin sheaths of nerves, whereas nonpolar lipids are generally associated with lipid reserves of animals. Therefore, if questions are asked about annual cycling of lipid stores of an animal, nonpolar solvents should be used so that extraction of polar lipids associated with body structures is minimized.

The choice of extraction techniques used for eggs is not quite as clear. Because triglycerides are the traditional storage lipids in adults, some authors have focused on nonpolar lipids in eggs to estimate parental investment in care (Kraemer and Bennett, 1981; Congdon et al., 1983a,c; Congdon and Gibbons, 1985). However, ques-

Table 8.1. Characteristics of *Trachemys scripta* and eggs

Plastron length at sexual maturity (mm)	Eggs							Region	Reference
	Length (mm)	Width (mm)	Length-width ratio	Wet mass (g)	Percent water ^a	Clutch size	N (eggs; clutches)		
--	36.4	22.2	1.64	10.5	72.2	7.1	489; 88	South Carolina	6
207	36.4	21.4	1.70	9.8	--	6.1	--; 42	South Carolina	4
150	36.0	22.9	1.57	11.0	--	9.6	--; 23	South Carolina	4
--	36.0	22.6	1.59	10.9	74.4	8.7	--; 33	South Carolina	5
240	42.2	28.2	1.50	20.7	--	17.4	87; --	Panama	3
205	34.3	23.2	1.48	10.8	--	10.2	--; 43	Virginia	7
158	36.2	21.6	1.68	9.7	--	9.3	221; 67	Illinois	1
159	37.7	22.6	1.67	11.1	--	7.0	406; 129	Louisiana	2
194	38.1	22.6	1.68	11.8	--	12.0	373; --	Southern Mexico	8
\bar{X}	187.6	37.0	23.0	1.60	11.8	9.7			

References: 1, Cagle, 1944; 2, Cagle, 1950; 3, Moll and Legler, 1971; 4, Congdon and Gibbons, 1983; 5, Caudle, 1984; 6, Congdon and Gibbons, 1985; 7, see Chapter 11; 8, see Chapter 13.

^aWater as a percentage of total egg wet mass, including shell.

tions remain about the ability of yolk reserves to be used for growth of hatchlings, so information about the polar lipids in eggs is also important (Caudle, 1984; Wilhoft, 1986). Thus, we recommend that both polar and nonpolar solvents be used in future studies of egg components so that the amount of both lipid classes can be determined. In addition, we recommend that, because of the variety of eggshell types among turtle species, the eggshell be removed prior to lipid extraction. Minimum data reported should include (1) the clutch size, body length, and wet mass of females producing the eggs; (2) the length, breadth, and total wet mass of fresh eggs; (3) the dry mass of shell and egg components as well as the masses of polar and nonpolar lipids and lean dry material; and (4) the percentages of each component.

Among populations of the slider turtle (*Trachemys scripta*), sexual maturity of females is attained at a plastron length (PL) ranging from 150 to 240 mm (Cagle, 1950; Moll and Legler, 1971; Gibbons et al., 1982; Congdon and Gibbons, 1983). Females reproduce at PLs ranging from 150 mm to more than 325 mm (Moll and Legler, 1971; Gibbons et al., 1982). Adult females from populations in the southeastern United States had PLs that ranged from 150 to 277 mm (Congdon and Gibbons, 1983). Among those females, egg wet mass and egg width, but not egg length, increased significantly with body size. When mean values were included for populations from the tropics (Table 8.1), essentially the same pattern persisted. Relationships of egg wet mass and egg width to body size were marginally significant, but egg length was not.

In a tropical slider population, egg length was used to explore the relationships of egg size to body size among turtles (Moll and Legler, 1971). The data presented in Table 8.1 and from Congdon and Gibbons (1983) indicate that egg width and egg wet mass exhibit stronger relation-

ships with body size of *T. scripta* than does egg length. Similar results have been found for both *Chrysemys picta* (Congdon and Tinkle, 1982b) and *Deirochelys reticularia* (Congdon et al., 1983a). It is a common observation among many groups of reptiles that clutch size increases as body size of females increases (Carpenter, 1960; Semlitsch and Gibbons, 1978; Dunham and Miles, 1985; Dunham et al., 1988a; Wilbur and Morin, 1988). Less frequently reported are incidences in which egg or neonate size increases with body size of females (Caldwell, 1959; Ewert, 1979; Moll, 1979; Stewart, 1979). Tucker et al. (1978) documented that egg size increased with body size in the painted turtle (*C. picta*) and suggested that egg size might be constrained by the size of the pelvic opening through which the eggs must pass. Since that time, evidence supporting pelvic constraint of egg size has been reported for *C. picta* and *D. reticularia* (Congdon and Tinkle, 1982b; Congdon et al., 1983a; Congdon and Gibbons, 1987).

In a study of three species of emydid turtles (*C. picta*, *D. reticularia*, and *T. scripta*), we found that pelvic constraint on egg size among the species appeared to be related to body size (Congdon and Gibbons, 1987). In two small-bodied species (*C. picta* and *D. reticularia*), egg size increased from the smallest to the largest gravid females, and the slopes of the lines relating egg size and pelvic opening width to body size were essentially equal. In contrast, eggs of female *T. scripta* increased with body size only slightly, relative to eggs of the other two species, and the slope of the line relating pelvic width to body size was five times steeper than the line relating egg width to body size. The constraint on egg size due to pelvic opening size in *C. picta* and *D. reticularia* apparently resulted in a situation that is not in accord with that predicted by optimal-egg-size models; that is, substantially more of the varia-

tion in reproductive output was due to variation in egg size than was found in *T. scripta*, where pelvic constraint did not exist.

Characteristics and Components of Turtle Eggs

Of the 12 species with oblong eggs that are described in Figure 8.4, 9 (75%), including *T. scripta*, had egg length-width ratios of 1.6 or 1.7. Only one large-bodied species (*Pseudemys concinna*, 1.5) and 2 small-bodied species (*Clemmys marmorata* and *Chrysemys picta dorsalis*, 1.9) had egg measurement ratios other than 1.6 or 1.7. The only pattern that is apparent in relation to egg shape (i.e., whether the eggs are round or oblong) is that only those turtles with relatively large body size have round eggs. The wet mass of *Gopherus polyphemus* eggs was approximately four times the wet mass of the largest of all other eggs. Water averaged 68.8% of the wet mass of all turtle eggs (Table 8.2).

The components of turtle eggs, and probably all reptile eggs, provide material and energy for two distinct, albeit continuous, aspects of early development. First, energy

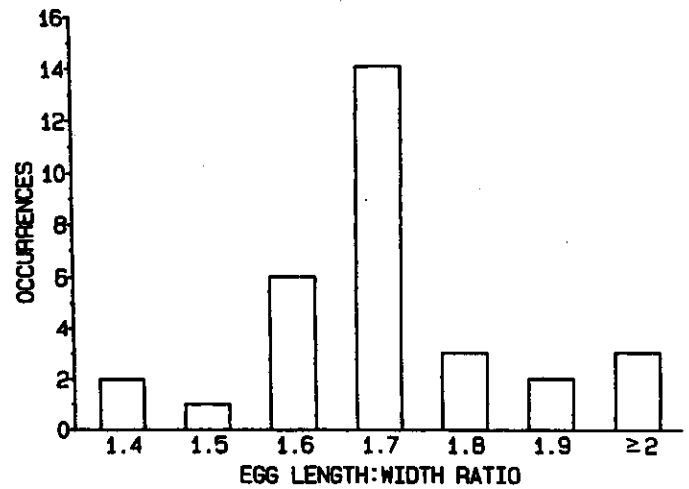


FIGURE 8.4. Frequency histogram of the ratio of egg length to egg width of 12 species of turtles with oblong eggs. Data are from Ewert (1979) and Congdon and Gibbons (1985).

Table 8.2. Egg characteristics of various species of turtles

Family and species	Eggs					
	Length (mm)	Width (mm)	Wet mass (g)	Percent water*	Clutch size	N (eggs; clutches)
Intermediate-shelled eggs						
Chelydridae						
<i>Chelydra serpentina</i>	--	25.8	9.6	68.3	23.6	73; 44
	--	--	9.4	72.6	--	139; 22
	--	--	10.4	70.6	44.5	400; 9
	27.2	11.2	--	34.0	--	--; 230
Flexible-shelled eggs						
Emydidae						
<i>Chrysemys picta dorsalis</i>	--	--	6.9	74.4	--	13; --
	17.3	33.2	6.2	66.5	--	5; 1
<i>C. p. marginata</i>	17.5	29.8	4.1	--	7.6	398; 77
<i>Deirochelys reticularia</i>	20.8	34.8	9.1	70.7	8.0	110; 13
<i>Emydoidea blandingii</i>	23.2	37.6	11.3	--	10.0	132; 20
<i>Malaclemys terrapin</i>	--	--	7.3	68.9	--	21; 7
<i>Pseudemys concinna</i>	23.9	36.4	12.0	72.8	--	15; 1
<i>P. floridana</i>	23.2	36.2	11.5	72.0	11.5	89; 11
<i>Terrapene carolina</i>	20.7	35.6	9.0	67.9	3.4	25; 8
<i>Trachemys scripta</i>	22.2	36.4	10.5	72.2	7.1	489; 88
Rigid-shelled eggs						
Emydidae						
<i>Clemmys marmorata</i>	19.1	37.3	8.3	71.2	--	6; 2
Testudinidae						
<i>Geochelone ymphora</i>	44.5	--	42.8	65.3	--	4; 1
Kinosternidae						
<i>Kinosternon flavescens</i>	16.6	26.9	4.3	65.9*	4.9	52; 10
<i>K. subrubrum</i>	15.6	26.2	3.9	61.2	3.4	66; 19
<i>Sternotherus odoratus</i>	15.5	27.1	4.0	64.5	4.5	36; 9
Trionychidae						
<i>Trionyx ferox</i>	--	26.7	10.4	70.7	--	15; 1

Sources: Lynn and von Brand, 1945; Obbard, 1983; Congdon and Gibbons, 1985; Wilhoft, 1986.

*Water as a percentage of total egg, including shell.

Table 8.3. Characteristics of dry components of *Trachemys scripta* eggs

Total mass	Shell			Lipids			Egg lean dry mass	Reference
	Mass	% of total egg	Yolk mass	Mass	% of yolk	% of total egg		
3.24	—	—	—	0.96 ^a	—	29.5 ^a	2.28 ^c	1
3.13	0.54	18.0	2.78	1.01 ^b	40.7 ^b	33.4 ^b	1.77 ^c	2
2.90	0.55	18.8	2.35	0.71 ^a	30.4 ^a	24.8 ^a	1.64 ^d	3

Note: Mass is given in g.

References: 1, Congdon et al., 1983c; 2, Caudle, 1984; 3, Congdon and Gibbons, 1985.

^aIncludes nonpolar lipids only.

^bIncludes polar and nonpolar lipids.

^cIncludes polar lipids and shell.

^dIncludes polar lipids.

^eIncludes no polar lipids.

and material are used within the egg for development and maintenance of the embryo, and, second, energy and material remaining in the hatchling yolk sac are used for maintenance and possibly for growth of the hatchling. The distinction between the two components of energy utilization is important in understanding the function of the reptilian egg (Kraemer and Bennett, 1981; Congdon et al., 1983a,c; Congdon and Gibbons, 1985; Wilhoft, 1986).

Eggs of *T. scripta* from South Carolina average 10.5 g in wet mass and 3.0 g in dry mass (Fig. 8.3, Table 8.2). The dry mass of the shell (0.55 g) averages approximately 18% of the dry mass of the egg (Table 8.3). Polar lipids (Caudle, 1984) and nonpolar lipids (Congdon and Gibbons, 1985) make up approximately 11% and 30% of the dry mass of the egg, respectively. The proportion of nonpolar lipids in the yolks of turtle eggs ranges from 23% (*Chelydra serpentina*) to 34% (*D. reticularia*) among species (Table 8.4).

The most complete analysis of the components of turtle eggs has been done on the snapping turtle (*C. serpentina*—Wilhoft, 1986). Wilhoft's study is unique in that, as far as we know, it is the only study that provides complete information on the proportions of polar and nonpolar lipids in turtle eggs. In the egg yolk of *C. serpentina*, 12.3% of the lipids are polar and 21.5% are nonpolar. Data on the polar lipids left in hatchling yolk sacs were not reported, but it would be interesting to know if proportionally more of the polar lipids, relative to the nonpolar lipids, are used during development. Wilhoft's statement that "for turtle eggs, the total extractable lipids as well as protein should be considered as total storage energy [for the hatchling]" should be carefully examined. First, if the question is related to total support of all immediate needs of the hatchling (e.g., maintenance, tissue maturation, and growth), then the statement may be valid if only the material in the yolk sac is considered. If lipids are also extracted from the body of the hatchling, using polar solvents (Wilhoft, 1986), then structural lipids from the hatchling bodies are

included as stored energy. If the question is asked just about support of maintenance for the hatchling, rather than tissue maturation or growth, then the nonpolar lipids are probably a better index of storage energy.

Two other aspects of turtle eggs—eggshell type and whether the hatchlings delay emergence from the nest—are apparently related to the relative proportions of egg yolk components. Because turtle eggs have two distinct shell types, it is necessary to examine egg components of each group for differences (Tables 8.2 and 8.4). The slope (0.41) of the line relating eggshell dry mass to the amount of nonpolar lipids in eggs with flexible shells was more than twice as steep as the slope (0.15) of the line for eggs with rigid shells (Congdon and Gibbons, 1985). The increased slope resulted from the combination of less inorganic material in the shells of flexible-shelled eggs (Lamb and Congdon, 1985) and a higher proportional yolk lipid content (33%) relative to yolks from eggs with rigid shells (26%; Congdon and Gibbons, 1985).

Two notable exceptions to the general comparison of lipid levels with shell types are *Terrapene carolina* (25.8% yolk lipids), which has a flexible-shelled egg, and *Kinosternon subrubrum* (31.6% yolk lipids), which has a rigid-shelled egg. Both are more similar in proportional yolk lipids to turtles with opposite eggshell types (Table 8.4; Congdon and Gibbons, 1985). Two apparent differences in these exceptions that may be important in determining lipid levels in their eggs is that *T. carolina* is the only terrestrial turtle with flexible-shelled eggs that was examined by Congdon and Gibbons (1985), and *K. subrubrum* is the only turtle examined that has rigid-shelled eggs and hatchlings that overwinter in the nest. Why the difference in eggshell type and lipid levels in turtle eggs should have any association remains an open question. However, it seems likely that differences in eggshell type are related to differences in water exchange between the egg and its environment (see Water Relations of Turtle Eggs during Development, below). An additional factor may be the length of time that the hatchling spends in the nest.

Table 8.4. Characteristics of dry components of eggs of various species of turtles and other reptiles

Family and species	Total dry mass	Shell dry mass	Nonpolar lipids			Egg lean dry mass	Region	Reference
			Mass	% of total egg	% of yolk			
Intermediate-shelled eggs								
Cheylridae								
<i>Cheylra serpentina</i>	2.59	0.77	0.60 ^a	16.2	33.8 ^a	1.22 ^b	New Jersey	7
	3.04	--	0.45	14.6	--	2.59 ^c	Michigan	3
	3.05	0.71	0.55	18.0	23.5	1.78 ^d	North Carolina	5
Flexible-shelled eggs								
Emydidae								
<i>Chrysemys picta</i>								
	2.07	0.41	0.54	26.4	33.0	1.11 ^d	Georgia	5
	1.78	--	0.32	22.7	--	1.11 ^c	Michigan	3
	1.86	--	0.42	22.8	--	1.44 ^c	Wisconsin	3
<i>Deirochelys reticularia</i>								
	2.46	0.49	0.62	25.2	31.5	1.35 ^d	South Carolina	2
	2.80	0.54	0.73	26.2	32.4	1.52 ^d	South Carolina	5
<i>Emydoidea blandingii</i>								
	3.55	--	0.55	15.6	--	3.00 ^c	Michigan	3
<i>Graptemys geographica</i>								
	2.51	--	0.40	15.9	--	2.11 ^c	Michigan	3
<i>G. ouachitensis</i>								
	2.56	--	0.62	24.4	--	1.94 ^c	Wisconsin	3
<i>Malaclemys terrapin</i>								
	2.24	--	--	--	26.4	--	New Jersey	1
<i>Pseudemys concinna</i>								
	3.24	0.51	0.76	23.3	27.7	1.97 ^d	South Carolina	5
<i>P. floridana</i>								
	3.41	0.60	0.80	23.7	29.0	1.96 ^d	South Carolina	5
<i>Terrapene carolina</i>								
	2.94	0.60	0.59	20.6	25.8	1.70 ^d	South Carolina	5
<i>Trachemys scripta</i>								
	3.24	--	0.96	29.5	--	2.28 ^c	South Carolina	3
	2.90	0.55	0.71	24.8	30.4	1.64 ^d	South Carolina	5
Rigid-shelled eggs								
Kinosternidae								
<i>Kinosternon flavescens</i>								
	1.65	--	0.43	26.1 ^a	--	1.22 ^c	Texas	6
<i>K. subrubrum</i>								
	1.53	0.67	0.27	17.7	31.6	0.59 ^d	South Carolina	5
<i>Sternotherus odoratus</i>								
	1.41	0.58	0.21	15.4	25.8	0.62 ^d	South Carolina	5
	1.94	--	0.23	11.8	--	1.71 ^c	Michigan	3
Trionychidae								
<i>Trionyx ferox</i>								
	3.05	0.96	0.58	19.2	28.0	1.51 ^d	Georgia	5
Crocodylidae								
<i>Alligator mississippiensis</i>								
	20.10	7.10	5.20	26.0	40.0	7.80 ^d	Florida	8
Anguillidae								
<i>Gerrhonotus coeruleus</i>								
	0.20	--	0.08	--	--	≈0.02	California	4
Colubridae								
<i>Nerodia rhombifera</i>								
	3.52	--	1.15	--	--	≈0.31	Oklahoma	3

Note: Mass is given in g.

References: 1, Ricklefs and Burger, 1977; 2, Congdon et al., 1983a; 3, Congdon et al., 1983c; 4, Stewart and Castillo, 1984; 5, Congdon and Gibbons, 1985; 6, Long, 1985; 7, Wilhoft, 1986; 8, Congdon and Gibbons, 1989b.

^aIncludes polar and nonpolar lipids.

^bIncludes no polar lipids.

^cIncludes polar lipids and shell.

^dIncludes lean polar lipids.

Hatchlings of *T. scripta* and a number of other species of turtles delay emergence from the nest (Bleakney, 1963; Goode and Russell, 1968; Gibbons, 1969; Gibbons and Nelson, 1978; Breitenbach et al., 1984). As a result, hatchlings that delay emergence are exposed during the first months of life to an environment that differs from that for hatchlings that emerge a short time after hatching. Preliminary data indicate that hatchlings that emerge from the nest upon hatching move to nearby aquatic habitats where they may forage until cold weather and remain during their first winter. In contrast, hatchlings that do not emerge from their nests spend their first winter in terrestrial nest cavities (Hartweg, 1944, 1946; Woolverton, 1961, 1963; Breitenbach et al., 1984). A comparison of the lipid levels of eggs of turtle species whose hatchlings

overwinter in the nest versus those of turtles that emerge upon hatching indicated that eggs of species with hatchlings that overwinter in the nest have a higher proportion of lipids (Congdon et al., 1983c; Congdon and Gibbons, 1985).

Two major features of these environments may be important in influencing the proportion of lipids in eggs and in the yolk reserves of hatchlings. First, hatchlings that emerge from a nest are exposed to water as soon as they reach an aquatic habitat during late summer or fall. Second, hatchlings that remain in the nest in northern latitudes have the potential to be exposed to temperatures below the freezing point of water (Woolverton, 1963; Breitenbach et al., 1984). Hatchlings remaining in nests and metabolizing lipids would benefit from the amount of metabolic water produced whether they were in nests in

southern or northern climates. Hatchlings at either latitude may require metabolic water to survive the extended time in the nest; however, the need for water as well as the amount of lipids metabolized at higher latitudes during winter would be low. In fact, desiccated tissue would be slightly more resistant to freezing than would well-hydrated tissues. In addition, hatchlings that delay emergence from the nest may use metabolic products of the additional lipids in the eggs to synthesize antifreeze compounds during winter. Although preliminary data do not indicate that hatchling *Chrysemys picta* (Breitenbach et al., 1984) can withstand temperatures below the supercooling limits of vertebrates (Lowe et al., 1971), further study is needed to determine the way egg components influence hatchling survival of winter temperatures in nests less than 10 cm below the surface at cold temperate latitudes.

Gas Exchanges among Embryo, Egg, and Nest

Gas exchanges between the embryo and the egg probably proceed from simple diffusion that is enhanced briefly by development of the vitelline circulation and subsequently by the allantoic circulation (Fisk and Tribe, 1949; Patten, 1958; Romanoff, 1967). Within a few days after eggs are first laid, their translucent shells begin to develop an opaque white patch at the top of the egg. This patch forms by partial drying of the shell and underlying membranes. Conductance of gases across the shell is low initially but increases as the opaque patch develops (Thompson, 1985). The increase in conductance is concomitant with increasing demands for gas exchange made by the developing embryo. Oxygen consumption by *T. scripta* embryos was higher for those incubated at 30° C through the seventh week than for those incubated at 26° C or 34° C (Fig. 8.5). However, during the seventh week, oxygen consumption rates were highest in embryos incubated at 26° C, followed by those incubated at 30° C and 34° C (Fig. 8.5).

These results seem to indicate that the rapid growth of embryos during the final stages of embryogenesis is inhibited by higher incubation temperatures. Oxygen consumption in the eggs of *Emydura macquarrii* increased 10 times, from almost 0.01 to approximately 0.1 cm³/h (STP), during approximately the first third of development, and then 5 times, to 0.5 cm³/h (STP), during approximately the second third of development. From 60% to 75% of the developmental period, oxygen consumption increased approximately 2.2 times, to 1.1 cm³/h (STP), whereupon it leveled off and then dropped slightly before the hatchling emerged from the egg (Thompson, 1985). The periods of development represented as percentages of the total developmental period roughly correspond to the developmental stages of tissue formation, organogenesis, and embryonic growth.

If developmental problems resulting from restricted gas

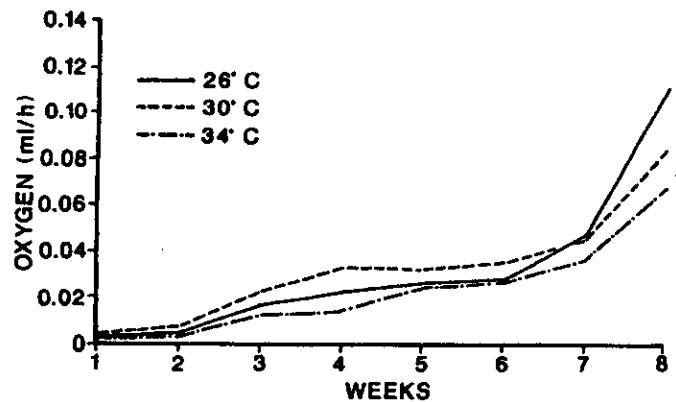


FIGURE 8.5. Oxygen consumption rates of *Trachemys scripta* eggs incubated at three temperatures.

exchange between the nest cavity and the surrounding soils occur, they should be most pronounced in the deepest nests, in nests laid in the most claylike soils, and in nests containing the largest mass of eggs late in development. For example, nests of *Chelonia mydas* with eggs that were within two weeks of hatching had oxygen levels 3% to 9% lower than the level in atmospheric air, and CO₂ levels increased 70 times, to 0.03% (Ackerman and Prange, 1972; Prange and Ackerman, 1974). The changes from atmospheric air were presumably caused primarily by the metabolic activities of the developing embryos, because the nests of *C. mydas* are usually in coarse sand, which may have relatively low microbe densities and resulting metabolic demands.

Nest plugs of *Chrysemys picta* constructed in clay soils have the consistency of a thick milkshake as a result of the female's voiding water onto the hard soil during the digging process (pers. obs.). Eggs of the tortoises *Chelodina longicollis* and *C. expansa* are sometimes placed in puddles of clay that harden and encase the eggs and subsequently the hatchlings (Goode and Russell, 1968). The effect of this encasement on gas exchange with the soil is unknown, but it can substantially delay emergence of the hatchling until rain softens the surrounding soil.

Another unexplored but potential problem with gas exchange in nests may occur for hatchlings that overwinter in nests where the ground freezes and snow cover is substantial (Breitenbach et al., 1984). Certainly much experimental work is needed to determine how nest site selection by the female might be translated into subtle effects on the quality and survival of her hatchlings.

Water Relations of Turtle Eggs during Development

Perhaps the best-documented manner in which eggshells of turtles differentially isolate the developing embryos from the external environment is the response of rigid and flexible eggshells to hydric conditions of the incubation

Table 8.5. Characteristics of hatchling *Trachemys scripta* incubated on substrates with different levels of hydration

Substrate	Carapace length (mm)	Wet mass	Dry mass	Yolk sac		Lipids			
				Dry mass	% lipids	Dry mass of some lipids	% of some mass	% of total hatchling mass	% of egg
Dry	28.7	6.72	2.30	1.04	34.5	0.24	19.0	26.1	59.5
Moist	30.9	7.73	2.27	0.64	39.3	0.34	20.9	25.8	57.5
Wet	31.2	8.04	2.14	0.48	40.8	0.32	19.9	24.5	52.0

Source: Caudle, 1984.

Note: Mass is given in g. Hatchlings were incubated on vermiculite that contained 19% water (dry), 40% water (moist), and 58% water (wet) by mass.

substrate. To a large extent the amount of isolation depends on the degree of calcification of the eggshell and the associated changes in shell morphology. Flexible-shelled eggs incubated on relatively moist substrates (approximately -150 kPa) absorb water (Cunningham and Hurwitz, 1936; Cunningham and Huene, 1938; Dmi'el, 1967; Tracy et al., 1978; Packard et al., 1980, 1981a,b, 1983, 1985, 1987; G. Packard et al., 1982; Morris et al., 1983; Gettinger et al., 1984; Packard and Packard, 1984a,b, 1986; Ackerman et al., 1985a,b; Gutzke and Packard, 1985; Gutzke et al., 1987; Thompson, 1987) and increase in mass over the first third to half of incubation. Flexible-shelled eggs incubated on relatively dry substrates (drier than -750 kPa) lose water, and thus mass, continually over the incubation period (Morris et al., 1983).

Position also affects water relations of flexible-shelled eggs. Not all eggs within turtle nests are in contact with the substrate. Those at the center of the nest may be entirely suspended by contact with other eggs and exposed to a hydric environment different from that of the eggs in contact with the substrate (Packard et al., 1981a). Position is obviously more important in nests of turtles that produce large clutches of flexible-shelled eggs (e.g., *Chelydra serpentina* and some sea turtles) and less important in species that produce small clutches (e.g., *Terrapene* spp., *Chrysemys picta marginata*, *Gopherus* spp.). However, even in nests of species with moderate-sized clutches of eggs (e.g., *Trachemys scripta* and *C. picta bellii*), eggs lowest in the nest appear to be better hydrated (Cagle, 1937; Carr, 1952; Legler, 1954; Ewert, 1979). Thus, if there is an adaptation to conserve water in relation to position, it would not necessarily be most likely to occur in species with large clutches of eggs but could also occur in small-bodied species that have relatively shallow nests.

In contrast to the mass of flexible-shelled eggs (Packard et al., 1979a, 1981a), the mass of eggs with rigid shells is relatively independent of position in the nest or of substrate moisture potential. The independence from substrate moisture potential by rigid-shelled eggs may be the factor that allows some turtles to bury their eggs only partially.

In eggs with flexible, porous shells, survivorship and development of embryos are influenced by the hydric environment of the incubation substrate because there is water exchange between the egg and the environment. In general, developmental abnormalities and mortality of embryos increase in eggs incubated on extremely dry substrates (Caudle, 1984). The degree of hydration of the incubation substrate influences the body size and mass that *T. scripta* hatchlings attain before leaving the egg (Table 8.5). Hatchlings that emerged from eggs incubated on wet substrates averaged 2.5 mm (8%) larger and 1.3 g (16%) heavier in wet mass than those incubated on dry substrates. However, the dry mass of hatchlings incubated on dry substrates averaged higher for both hatchling body (0.16 g, 9%) and yolk sac (0.56 g, 46%). The dry mass figures indicate that hatchlings incubated on wet substrates have grown earlier in the incubation period and converted more of the original egg mass to hatchling tissues. As a result, these hatchlings experienced higher maintenance costs that were concomitant with earlier growth and larger size. In contrast, hatchlings incubated on dry substrates had a higher dry mass upon hatching because they grew less rapidly, they had smaller maintenance costs, and more of their mass was composed of original yolk material.

In summary, embryos incubated in moist environments use more of the egg material, hatch at larger sizes, and have smaller yolk stores (Tracy et al., 1978; Packard et al., 1980, 1981a,b, 1983, 1985, 1987; G. Packard et al., 1982; Morris et al., 1983; Gettinger et al., 1984; Packard and Packard, 1984a,b, 1986; Ackerman, 1985a,b; Gutzke and Packard, 1986; Gutzke et al., 1987; Thompson, 1987). In contrast to embryos in flexible-shelled eggs, survivorship and growth patterns of embryos that develop inside rigid-shelled eggs tend to be relatively insensitive to the hydric conditions of the incubation substrate (Packard et al., 1979a, 1981a).

Eggs of *C. picta* contained an average of 104.8 mg of calcium, with 0.1 mg, 7.1 mg, and 97.6 mg found in the albumin, yolk, and eggshell, respectively (Packard and Packard, 1986). Calcium used for development of the em-

bryo came from both the yolk and the eggshell and was influenced by hydric conditions during development (Packard et al., 1984a,b, 1985; Packard and Packard, 1986). Embryos incubated on wet substrates obtained most of their calcium from the eggshell (56%) and the egg yolk (40%). Less than 1 mg of calcium remained in the yolk reserves of hatchlings incubated on either wet or dry substrates (Packard and Packard, 1986).

The conclusion that the calcium level in yolk reserves of hatchlings could not support the growth of soft tissue (Packard and Packard, 1986) seems unfounded. If we assume that the calcium content in muscle tissue of a *C. picta* hatchling weighing 4 g is similar to that of a fish (0.43 mg calcium/g wet mass of muscle; Agnedal, 1967), then the hatchling could add approximately 2 g (50% of its body mass) before depleting the calcium in the yolk reserves. Whether hatchlings do use yolk reserves for growth remains to be demonstrated. Yolk reserves available to hatchlings (Kraemer and Bennett, 1981; Congdon et al., 1983a,c; Wilhoft, 1986) are used by the hatchling for maintenance metabolism and may also be used to promote tissue maturation and growth of soft tissue, but probably not growth of skeletal tissue.

Hatchlings resulting from embryos that either developed earlier or developed more completely by delaying emergence from the egg should have more tissue mass developed or more mature tissues. Because the egg is a closed system in terms of chemical potential energy, the maintenance costs associated with a greater tissue mass or with maintaining an equivalent tissue mass for a longer time should be higher and, by definition, should result in less residual yolk at the time of hatching. Thus, the larger yolk stores in smaller hatchlings may be beneficial (relative to a similarly small hatchling with lower reserves) but should not be considered an adaptation. Rather, the larger stores are the result of constraints on the developmental processes that took place within the egg. This view is supported by the evidence of improved running speed on land and swimming speed in water of hatchling snapping turtles that were incubated on wet, rather than dry, substrates (Miller et al., 1987).

The pattern of changes in turtle hatchling characteristics in response to variation in the incubation environment appears to be a general pattern in reptiles (Muth, 1980; Andrews and Sexton, 1981; Stewart and Castillo, 1984; Gutzke and Packard, 1986). Turtle eggs incubated at lower temperatures take longer to hatch than those incubated at higher temperatures. However, species vary considerably in the length of incubation (Ewert, 1979, 1985). Slider turtle eggs can complete the incubation process in approximately two to three months, depending upon the temperature, although variability can be high at any temperature regime (e.g., days to emergence from egg in laboratory experiments ranged from 67 to 104 [\bar{x} = 81; N = 27] at temperatures of 29°–31° C).

Eggs and Evolutionary Concepts

In preparation for reproduction, a female must make three major "determinations": (1) the total amount of energy available for present reproduction, (2) the quantity of energy to be allocated to each offspring, and (3) the number of individuals that can be produced by the present level of investment in each offspring. The three determinations fall roughly into the conceptual categories of reproductive effort (RE), parental investment (PI), and optimal egg size (OES).

Within overall life history theories is a subset of models that describe how an organism should apportion its finite resources among the competing compartments of maintenance, growth, and reproduction. Central to these theories is the concept of reproductive effort, or that portion of an animal's resource budget that is allocated to reproduction (Fisher, 1930; Hirshfield and Tinkle, 1975), a concept that does not directly pertain to egg size or quality.

All of the energy allocated to each individual turtle hatchling is contained within the egg. Because of this, the concepts of parental investment and optimal egg size are more tightly coupled for turtles than for mammals and birds, which provide extended parental care such as guarding and feeding of young. Thus, for turtle eggs it is important to separate the investments made for embryonic development from those made for fueling the hatchling after it leaves the egg (Table 8.6).

The interactions between determinants of offspring numbers and size or quality of offspring have been considered for some time (Darwin, 1859). More recent considerations have centered on the idea that organisms should invest in offspring at the level that maximizes the fitness of the parents (Lack, 1947, 1948, 1954b, 1968; Svardson, 1949; Williams, 1966a). There are presently two major categories of evolutionary theories (i.e., optimality or canalization theories and developmental plasticity theories) that attempt to explain the range of variation in egg size either within or among females. Morphological constraint on egg size has also been offered to explain some of the variation in turtle egg size.

Optimal-egg-size models (Williams, 1966; Smith and Fretwell, 1974; Brockelman, 1975; Parker and Begon, 1986) attempt to describe the relationships and interactions between egg size and number. The models make the

Table 8.6. Percent lipids found in various species of hatchlings upon leaving egg

Species	Nonpolar lipids	Total lipids
<i>Chelydra serpentina</i>	12.9	29.2
<i>Chrysemys picta</i>	14.7	--
<i>Deirochelys reticularia</i>	27.4	--
<i>Emydoidea blandingii</i>	14.7	--
<i>Trachemys scripta</i>	--	24.5

following assumptions: (1) Parents have a limited amount of resources and energy available for a given reproductive bout; (2) a minimum amount of energy is required to produce viable offspring; and (3) the gain in fitness of offspring is not linear with the amount of parental investment, that is, there is a level at which a given investment in offspring results in large gains followed by a level of investment for which minimal or no increase in the fitness of offspring occurs (also see Pianka, 1974; Schaffer and Gadgil, 1975). If the first assumption is true, it follows that as the amount of energy invested in individual offspring goes up, the number of individuals produced must be reduced. However, if some factor other than absolute energy availability exists (e.g., morphological constraints such as volume of a turtle's body cavity or size of the pelvic opening), then results inconsistent with predictions from OES models can be obtained.

A major prediction from OES theory is that within a population the amount of variation in reproductive output among females should result primarily from variation in the number of offspring produced and secondarily from variation in egg size. One problem is that the actual level of variation in reproductive output due to variation in egg size that is acceptable under OES models has not been defined in either relative or absolute terms.

In contrast to OES theory, other investigators have proposed that natural selection should favor developmental plasticity that results in a range of reproductive characteristics when environmental variability is unpredictable (Robertson, 1971; Capinera, 1979; Kaplan, 1980; Cooper and Kaplan, 1982; Caswell, 1983; Kaplan and Cooper, 1984). Within these models, variation in egg size should occur within a single reproductive bout or among reproductive bouts within a single year (Kaplan and Cooper, 1984). We expect that there are life history traits and environmental conditions that could result in either strategy, and the existence of support for one theory does not necessarily refute the other.

Regardless of the type of reproductive tactic used by females, two factors must be considered when attempting to understand the functions and evolution of the eggs of turtles and probably all reptiles. It has been argued that the eggs of turtles and other reptiles should be viewed as two distinct components of a single system in which energy is allocated by the female for (1) embryogenesis and (2) extended parental care in the form of yolk reserves that remain in the egg after hatching (Kraemer and Bennett, 1981; Congdon and Tinkle, 1982b; Congdon et al., 1983a,c; Troyer, 1983; Wilhoft, 1986; Congdon and Gibbons, 1987; Congdon and Gibbons, 1989b). Considering turtle eggs as a two-component system points out some problems with existing definitions of parental investment. Specifically, PI should identify how the investment is to be used by the offspring and at what developmental period the investment is made by the parent.

Trivers (1972) defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." This definition was modified (Trivers, 1985) and stated as "anything done for the offspring, including building it, which increases the offspring's reproductive success at a cost to the remainder of the parent's reproductive success." Both statements yield essentially the same definition of PI. For both, the benefit to the parent is measured in units of reproductive success of the offspring that receive the PI, and the cost to the parent is in units of reduced reproductive success of future or other offspring.

We find two problems with Trivers' definition. First, both categories of investment, that used for embryogenesis and that used for fueling the developed hatchling, fall under the overall category of PI. The definition is adequate for attempts to model optimal egg size in which it is assumed that all of the PI is used to make a larger offspring (Parker and Begon, 1986) rather than providing it with post-hatching reserves. We suggest that by lumping together both categories of investment in an egg, Trivers' definition obscures important ecological and evolutionary questions about distinct processes that proceed in different ways toward the common goal of making a successful offspring. Second, we suggest that if all energy allocated to a single egg is to be considered PI, the trade-off between offspring that is implicit in Trivers' first definition is very narrow; i.e., there is no trade-off between competing offspring but rather only a "decision" to make offspring A rather than make offspring B. We at least need new terminology to distinguish between the two energy compartments that make up reptile eggs.

For the rest of the discussion of PI in reptile eggs, we will separate the investments made by the parent into (1) the energy invested in making a complete embryo (PIE) and (2) the energy invested by the female for parental care (PIC), that is, energy in excess of that needed to produce a complete hatchling (either hatching from an egg or the product of live birth), in the form of a yolk sac or hatchling fat bodies, that is used by the hatchling after it leaves the egg. We assume that a portion of the energy allocated to an egg by the female is done expressly to fuel the hatchling. Because data on turtles and other reptiles indicate that the material, lipids, or energy left in the yolk sac when the hatchling leaves the egg or is born usually exceeds 50% of the original energy in the egg, this investment is far from trivial (Kraemer and Bennett, 1981; Congdon and Tinkle, 1982b; Congdon et al., 1983a,c; Troyer, 1983; Stewart and Castillo, 1984; Wilhoft, 1986; Congdon and Gibbons, 1989b). This assumption could be shown to be incorrect by demonstrating that hatchlings incubated under what could be considered optimal conditions hatched with no residual yolk sac and formed no fat bodies. In this

case all of the material in the egg would be in the form of hatchling tissues or waste products (i.e., all of the material in the egg would be used for embryogenesis).

The second problem of terminology associated with PI is that of identifying the portion of the developmental process during which PIC is made. Parental investment in care should be identified as investments made before ovulation, during intrauterine development, or after gestation or egg laying (Kaplan, 1980; Congdon and Gibbons, 1985; Congdon and Gibbons, 1989b). These distinctions are important because not all options are open to parents at each stage of development. For example, pre-ovulatory PIC is made before the egg is ovulated and fertilized; therefore, matching unequal investment to differences in the complete genotype of the offspring is impossible. Investment during the intrauterine period or after birth of individuals allows the parent to invest selectively and unequally in its offspring in such a way that the parent's fitness is enhanced at the expense of some of her offspring's.

Eggs of the Slider Turtle: An Overview

Based on our own and other studies on slider turtles and other freshwater species, egg development in the slider turtle proceeds in the following manner. The follicles of an adult female are smallest following ovulation of the last clutch during the egg-laying season and begin to enlarge during late summer or early fall. Most or all of the energy allocated to the first clutch during the egg-laying season comes from that harvested during the previous summer and fall. Two or more clutches may be laid by an individual female in a single season, with a minimum of approximately two weeks between clutches. Energy for clutches subsequent to the first one is presumed to be acquired primarily from that harvested during the egg-laying season, but documentation for this hypothesis is lacking. Sliders, like most other species of turtles, construct nests in sites that are exposed to sunlight during a portion of the day. Soil temperatures, moisture, and texture are critical to incubation rate, embryo survivorship, and even sex ratio within the clutch and can be influenced to some degree by the female through choice of nest site location and depth of the nest. However, whether the female takes a conscious or inherent role in such determinations is yet to be demonstrated.

The composition and construction of the eggs of slider turtles are characteristic of the order Testudinata. The eggshell of turtles is composed of calcium carbonate in the form of aragonite rather than calcite, as in most other reptiles and birds. However, the eggshells of some turtles, such as the slider, are flexible, whereas some species have rigid eggshells with interlocking units. The variations in structure of flexible and rigid eggshells do not follow phy-

logenetic lines but may be associated with nest site substrates. However, the evolution of eggshell types of turtles as an adaptation to particular nest site characteristics has not been satisfactorily demonstrated. The eggshell of the slider turtle constitutes approximately 18% of the dry mass of the egg and is similar to that of other species that produce flexible-shelled eggs. Among species with rigid-shelled eggs, the shell may make up more than a third of the total egg dry mass. A major difference associated with shell types is in the patterns of growth and development of embryos in response to varying amounts of soil moisture. Embryos from rigid-shelled eggs are not appreciably affected by substrate moisture conditions, whereas hatching size of embryos from flexible-shelled eggs is significantly larger in moist substrates.

The harvesting and storage of energy by female turtles, and the timing and proportional allocation of lipid reserves to eggs, are critical to understanding the evolution of hatchling development. The lipid component of turtle eggs can be partitioned into polar and nonpolar lipids. Both types should be determined if possible when considering egg components. In addition, the clutch size, female size, and wet and dry mass of the shell and other egg components should be determined when addressing questions of parental investment.

The eggs and hatchlings of many species of turtles remain in the nest for several months after incubation is complete. Eggs of species such as the slider turtle that have hatchlings that delay emergence from the nest have higher proportions of lipids. One suggestion for these higher lipid reserves is that they may be used in some way to synthesize antifreeze compounds in winter.

The concepts of reproductive effort, parental investment, and optimal egg size all center around how individual females allocate energy within and among clutches. Research with turtles has permitted challenges to and reconsideration of some life history models (e.g., optimal egg size and morphological constraint). We consider turtles to be ideal organisms for addressing a number of evolutionary concepts regarding eggs because of the group's consistency in total oviparity and long incubation period, extreme iteroparity, and lack of post-ovipositional parental care in natural situations. We anticipate great strides during the next few years by turtle biologists interested in eggs and evolutionary concepts.

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