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The Evolution of Turtle Life Histories

Abstract

How turtles evolved traits that are primarily related to survivorship and reproduction is explored within the framework of evolutionary theories of senescence and life history development. The evolution of a protective bony shell in the Testudines more than 200 million years ago apparently resulted in lowered mortality rates of adults, which allowed them to live long enough to have senescence deleteriously affect their reproductive capabilities. Consequently, genes that either postponed or reduced the expression of senescence were favored. A scenario is presented that suggests that turtle life history traits are more consistent with the antagonistic pleiotropy theory than with the mutation accumulation theory of senescence. Indeterminant growth, age and size at sexual maturity, clutch size, and egg size of turtles are discussed in relation to five hypotheses of the evolution of delayed sexual maturity and iteroparity.

Introduction

Turtles have been identified as being the epitome of long-lived organisms (Williams, 1957; Tinkle, 1969; Wilbur and Morin, 1988) and paragons of delayed sexual maturity, longevity, and iteroparity, that is, repeated cycles of reproduction (Wilbur and Morin, 1988). The slider turtle (*Trachemys scripta*) is one species of turtle for which the traits of extended longevity, delayed sexual maturity, and both annual and interannual iteroparity have been well documented in natural populations (Cagle, 1946, 1950; Gibbons et al., 1981, 1982; Gibbons, 1982, 1987; Gibbons and Semlitsch, 1982). Thus, turtles in general, and *T. scripta* in particular, are model organisms for an exploration of concepts related to theories of life history evolution and the evolution of longevity.

All issues related to the processes of life history evolution of either short- or long-lived organisms derive from the following question paraphrased from the insights of

Williams (1957) on the evolution of senescence. Why is it that after achieving the seemingly miraculous feat of morphogenesis, a complex metazoan is unable to perform the apparently much simpler task of merely maintaining that which is already formed? However, when the range of longevities of sexually reproducing organisms is considered, it is an inescapable conclusion that turtles do a much better job of maintaining their soma through time than do many other organisms. Among reptiles there exist relatively short-lived groups, such as most lizards and some snakes, and relatively long-lived groups, such as turtles, crocodylians, and other snakes. Although the extremes of reptile longevities represented by squamates versus turtles present an opportunity to attempt to answer the question posed above, the major emphasis in this chapter will be to examine life history traits of turtles in relation to the evolutionary theories of senescence and life histories.

To accomplish this goal it is necessary (1) to explore current concepts and theories related to the evolution of life histories and senescence that will enhance our understanding of the evolution of longevity and (2) to determine which traits are particularly pertinent to the evolution of delayed reproduction, iteroparity, and longevity of turtles.

We will not attempt to review all life history theory literature or catalog the data on turtle life history characteristics. Rather we will concentrate on features that appear to have been necessary for the evolution of longevity. We will consider how these traits arose and how they are associated with other traits within a life history. Unfortunately, the lack of complete life history data on turtles, and on long-lived organisms in general, limits inference about the evolution of longevity. Additional data will be necessary to address the problem fully. Nevertheless, the reader is referred to two syntheses of turtle life histories that have succeeded notably despite the paucity of complete life history data (Moll, 1979; Wilbur and Morin, 1988).

Although our emphasis is on turtles and their characteristic of extended longevity, comparisons with relatively shorter-lived reptiles will be made where they may enhance our understanding of the processes that led to longevity. Detailed discussions of life history evolution of lizards and snakes can be found in the following papers (Tinkle, 1969; Tinkle et al., 1970; Congdon et al., 1982; Ballinger, 1983; Dunham and Miles, 1985; Parker and Plummer, 1987; Seigel and Ford, 1987; Dunham et al., 1988a). General reviews of life history theories and concepts are outlined in articles by Stearns (1976, 1977) and Williams (1966a,b).

Turtles have several characteristics that make them good models for the study of life histories of long-lived, iteroparous species. Probably the most important is that an individual can be marked as a hatchling with a unique code that is essentially permanent throughout the turtle's

lifetime. Other characteristics include the following: (1) Many turtles occur in relatively discrete populations at densities high enough to allow adequate numbers of individuals to be monitored throughout their lives; (2) eggshells are calcareous, and thus reproductive output of females can be nondestructively and repeatedly determined using x-radiography (Gibbons and Greene, 1979); (3) many turtles are of sufficient size to allow attachment of single-channel or multichannel radiotransmitters that monitor an individual's location and potentially other variables over long periods. In addition, two relatively recent nondestructive techniques—ultrasound tomography and the use of lipid-soluble gases to determine whole-body lipids—provide an opportunity to measure energy relations of turtles accurately for the first time.

Mark-recapture studies, in conjunction with some of the techniques mentioned above, have the potential to yield accurate age-specific data important to testing life history theories. Furthermore, if these studies are continued over a sufficient time, they should provide answers to questions about senescence in turtles.

Life History Traits

A life history is a suite of coevolved characteristics that directly influence population parameters. Life history traits include age-specific survivorship and reproductive output (clutch size and frequency), age at maturity, and longevity. Turtles exhibit a relatively narrow range of variation in life traits relative to lizards or snakes. For example, turtles have not evolved viviparity or complex postovipositional parental care. Whereas some aspects of turtle reproductive biology, ecology, and life history traits are relatively well known, there is a dearth of complete life history information on any given species. For example, to our knowledge only three life tables have been reported for freshwater turtles (Wilbur, 1975a; Tinkle et al., 1981; also see Chapter 15), and two of these involve the same population of *Chrysemys picta* from Michigan (Wilbur, 1975a; Tinkle et al., 1981).

The significance of demographic studies in testing predictions of life history theories stems from the following realization: Life history traits, like other phenotypic characteristics, evolve because they endow their possessors with higher individual fitness than alternate traits possessed by conspecifics within a population. In field studies, fitness can best be measured in terms of relative reproductive success, which largely depends on traits such as age and size at maturity, the proportion of assimilated energy devoted to reproduction, survivorship of offspring to reproductive age, and survivorship of individuals from one reproductive period to the next. These characteristics are exceptionally difficult to determine, and the problem is compounded because the necessary scrutiny of individuals of long-lived species must by definition be of long

duration. In fact, the following observation about reptiles and amphibians may have arisen with turtles in mind: ". . . in the larger forms the life-cycle is so easily modified by diapause, diet, temperature, and the like that individuals probably age at rates so different as to be beyond the access of actuarial statistics except in an experiment of intolerable length" (Comfort, 1979).

Senescence and Life Histories

In simplest terms, senescence is the process of becoming old. The process of aging is identified by the accumulation of physical and physiological traits that reduce the effectiveness of the individual in some manner related to reproduction or survival. We concur with the assumption made by Williams (1957) that expression of traits related to senescence is unavoidable and is, in most if not all cases, opposed by natural selection. Two not mutually exclusive evolutionary theories of aging provide a potential answer to the question posed earlier about the difficulty organisms have in maintaining their soma.

The theory of mutation accumulation refers to the accumulation of alleles arising through mutation that have deleterious effects expressed late in life, a time when natural selection has minimal effect on reducing their frequency of expression (Bidder, 1932; Haldane, 1941; Medawar, 1952; Edney and Gill, 1968). Proponents of the mutation accumulation theory argue that the ability of natural selection to influence the frequency of mutations leading to senescence is weak, because most individuals in natural populations die of extrinsic causes before traits of senescence are expressed. In cases where deleterious effects of aging are expressed, Medawar (1952) hypothesized the existence of modifier genes (age-of-onset modifiers) that would suppress the expression of senescence traits as long as possible.

According to the theory of antagonistic pleiotropy, genes that are favored by selection early in life, when natural selection has the greatest impact, have cumulative deleterious effects later in life, when natural selection is less effective at postponing or masking their expression (Williams, 1957, 1966a). Williams (1957) envisioned pleiotropy to result when the same genes have different effects on fitness at different ages because of changes in the somatic environment. Eventually, as the cumulative effects of pleiotropic genes become expressed earlier and begin to interfere with an earlier, and thus larger, portion of the total reproduction of the individual, opposition by natural selection to further accumulations would increase. There is no apparent reason that selection for age-of-onset modifiers (Medawar, 1952) could not function to modify pleiotropic genes (Mertz, 1975). The more important a gene is in the expression of senescence, the more strongly selection should act through modifiers to reduce or delay unfavorable effects (Williams, 1957). As suppres-

sion of the deleterious effects is realized, selection pressure for further reduction would diminish so that complete suppression would be difficult.

Williams extended his argument by stating, "Senescence should always be a generalized deterioration, and never largely due to changes in a single system." In many organisms the deterioration associated with aging occurs throughout most body systems and thus appears to result from the action of many genes. However, recent work on fruit flies (*Drosophila*) suggests that in some cases delayed senescence may be under the control of a single factor (Luckenbill et al., 1987). Rose and Charlesworth (1980, 1981) examined long-lived stocks of *Drosophila* for evidence of accumulated mutations, but their data supported the trade-offs predicted by antagonistic pleiotropy. However, Service et al. (1988) found evidence that mutation accumulation and antagonistic pleiotropy were involved in the evolution of senescence in *Drosophila*. Further expansion, development, and clarification of senescence theories have been made by Charlesworth (1980), Hamilton (1966), Kirkwood (1985), and Rose and Hutchinson (1987).

Life span has been both extended (*Drosophila*—Clark and Maynard Smith, 1955; Wattiaux, 1968) and reduced (*Tribolium*—Sokal, 1970; Mertz, 1975) by selection experiments. In general, age at sexual maturity is correlated with life span (Cutler, 1978). We propose that the correlation of age at sexual maturity with life span is more consistent with the antagonistic pleiotropy theory of senescence than with the mutation accumulation theory. If accumulation of random mutations causes senescence, then age-of-onset modifiers or genes that reduce expression of the accumulated mutations would operate randomly with regard to age. Therefore, modifier genes would not necessarily be restricted to acting directly on the expression of genes associated with a particular ontogenetic stage. However, assuming antagonistic pleiotropy, both age-of-onset and suppression genes would only modify the expression of genes involved in both early and late life processes. It is hard to envision modifier genes, acting on critical metabolic processes necessary at all ages, that could be precise enough to suppress the expression of traits late in life without also modifying their expression early in life.

We propose the following scenario, which seems particularly appropriate in a chapter on turtles, based on the original example of pleiotropic effects of genes related to calcium metabolism presented by Williams (1957). In a turtle, a mutation occurs that has a favorable effect on calcium metabolism, resulting in rapid growth, attainment of sexual maturity, and increased protection due to faster shell development. Later in life, the gene promotes calcification of connective tissue in arteries. Senescence, in this example, is the result of two opposing selective forces. The first is driven by a high probability of mor-

tality of adults to favor rapid growth and early attainment of sexual maturity at the expense of vigor later in life. The second selective force results because protection afforded by the shell allows adults to survive long enough to become harmed by calcification of arteries. In older individuals selection would favor age-of-onset modifiers and suppression genes that modify arterial calcification. Perfect modification would be restricted to gene expression related to calcification of arteries that occurs late in life. However, in a less precise natural system, the modifiers also exert a negative influence on calcium metabolism early in life. Modifications that influence the early expression would result in reduction of growth, postponement of sexual maturity, and a delay in protection provided by shell calcification.

From the above discussion, two considerations appear important if we are to understand the evolution of life histories of long-lived organisms. First, we must identify how traits or conditions arise that allow an organism to break the barrier of high extrinsic adult mortality and subsequently experience higher relative reproductive contribution later in life. Breaking this barrier appears to be a critical step in the evolution of longevity because under conditions of high extrinsic mortality of adults, natural selection seems to be biased in favor of youth over old age whenever a conflict of interest exists (Medawar, 1952; Williams, 1957). Age at death is important only insofar as it influences births or, more precisely, the proportion of early versus later births of individuals. Second, we need to identify how life history alternatives result in traits that are presently maintained and associated with long-lived organisms.

Mechanisms for Reducing Adult Mortality

Organisms may experience low adult mortality under the following conditions: domestication (horses, dogs, cats), armor (turtles); flight (birds, bats); noxiousness or poisonousness (plants, snakes); aggressiveness (carnivores); size (elephants, whales); sociality (primates); encephalization (primates); cryptic coloration (lizards, snakes). On occasion, specific environmental conditions in which predators are few or absent (e.g., certain insular settings) can result in reduced adult mortality. Of these traits or conditions, those that appear to be associated with longevity fall into three categories that lie along a gradient of increasing apparent costs: (1) no costs should result from domestication or living on islands in the absence of predators; (2) minimal costs might result from being cryptic, secretive, noxious, or poisonous; and (3) large costs should result from the development and maintenance of armor, flight, aggressiveness, or intelligence. Animals that become domesticated and are not used for food (pets such as dogs, cats, and horses) and prey species that colonize islands

could abruptly begin living long enough for the expression of senescence traits to become a cause of mortality. A striking example of extended longevity within a group involves insular populations of the gecko *Hoplodactylus duvauceli* that were marked in 1956 and 1959; individuals recaptured in 1968 had minimum ages of 13 and 19 years (Barwick, 1982). These geckos live longer and take longer (up to 7 years) to reach sexual maturity than do closely related species on the mainland. In this case, extended longevity bears no apparent costs to the animals involved because the initial change was strictly environmental.

In contrast, adult mortality can be reduced as a consequence of changes in the species itself. Animals that adopt behaviors such as reduced activity to escape predation may incur indirect energy costs associated with restricted resource acquisition due to reduced time and activity budgets. Alternatively, energy costs are directly involved in synthesis of noxious or toxic chemicals used for defense from predators. Animals that adopt armor, flight, aggressiveness, or intelligence to reduce mortality, however, may invest a relatively large amount of energy and time that could result in postponement of sexual maturity.

Fossil records indicate that armor has been a trait of turtles since they arose in the Triassic period about 200 million years ago. The shells of turtles certainly reduce their vulnerability to many predators, accidental injuries, and adverse environmental conditions. Yet, even the shell of a relatively small adult turtle may have required a major investment in time and energy to become fully functional in a protective sense. However, even relatively small-bodied turtles may live up to twice as long as some crocodylians (Comfort, 1956). The records of great delays in longevity (Swingland and Lessells, 1979; Gibbons and Semlitsch, 1982; Congdon et al., 1983b; Turner and Berry, 1986) and sexual maturity (Gibbons et al., 1981; Congdon et al., 1983b, 1987; Turner et al., 1987) that have been reported for turtles in the wild may both be associated with the investment required to obtain a maximum ambit of protection from armor.

For individuals, the shell's effectiveness increases with body size and increased calcification that occurs with age. Thus, the shells of modern turtle species appear to function more effectively in the protection of adults than of hatchlings and juveniles. However, as long as the increase in reproduction later in life compensates for the decrease in early reproductive success of individuals that delay reproduction, any benefit derived from even small increases in protection from the shell early in life would also be strongly favored.

It may seem unlikely that the intermediate stages of shell development would be effective against the array of large predators that existed and still exist on most continents. However, for armor to evolve, it would have to be effective not against all predators but against only those

responsible for a biologically significant portion of the mortality. Thus, it seems most likely that specialized armor would evolve today only in isolated settings with predator types reduced to one or a few of a specific type.

One problem that arises in the consideration of many evolutionary phenomena is that current traits are reflective of former conditions, so their function is no longer in the original context. A modern paradox exists with turtles in this regard. In contrast to an increase in survivorship associated with larger size, a special case exists when man acts as a major, highly selective predator. Ironically, the large body size and high fecundity of some turtles have resulted in increased death rates of adults and, in some species, of the embryos as well. A decrease in the protection that may have resulted from large body size has certainly increased rapidly in relatively recent times with the advent of commercial exploitation of eggs and meat of turtles in many regions of the world (King, 1982; Ross, 1982).

Indeterminant Growth

An early hypothesis advanced for fish (Bidder, 1932), but also applicable to turtles, suggested that senescence in vertebrates is caused by growth mechanisms that continue to operate after growth of the organism has ceased. Therefore, species that exhibit indeterminant growth would not exhibit traits of senescence, whereas those with determinant growth would. Subsequently, observations made on small teleost fishes indicated that senescence does occur even though growth continues past the onset of reproduction (Gerking, 1957). Although the hypothesis of Bidder (1932) was not supported as an all-or-none process, the association of a more rapid senescence rate with determinant growth has been documented (Comfort, 1956). These observations seem consistent with the aforementioned predictions of Medawar (1952) and Williams (1957).

Following the arguments of Bidder (1932), Comfort (1956), and Williams (1957), indeterminant growth can function within a population of turtles in a variety of ways to allow natural selection to oppose senescence by increasing the proportion of reproductive success, and in some cases the quality of offspring, that results from late reproduction. Some of the ways that larger body size may increase a turtle's reproductive output later in life have been well documented: for females, increased clutch size (Cagle, 1950; Moll and Legler, 1971; McPherson and Marion, 1981a; Tinkle et al., 1981; Gibbons et al., 1982; Congdon et al., 1983a, 1987; also see Chapter 9) and increased size or quality of eggs and thus neonates (Tucker et al., 1978; Congdon and Tinkle, 1982a; Congdon et al., 1983a; Congdon and Gibbons, 1985, 1987); for males, greater protection during terrestrial excursions in

search of females for mating (Gibbons, 1986). In addition, increased survivorship associated with larger size of adults has often been suggested, but not documented, in turtles.

A pattern contrary to expectation seems to exist in data on the relationships among reproductive characteristics, age, and body size within populations of adult slider turtles (*T. scripta*). The slider turtle and many other turtle species as well exhibit indeterminant growth (but see Andrews, 1982). Therefore, the size of a growing individual must be correlated with its age (i.e., because growth takes time, individuals become older as they grow larger). The relationship between time and growth suggests that age and body size should be related. However, among slider turtles, clutch size is more strongly correlated with body size than with age (Gibbons, 1982). A possible explanation is suggested for this apparent discrepancy when growth rates of juveniles are considered. Growth rates of juvenile turtles and most other organisms are higher than those of adults. In addition, the variation among individuals in the growth rate of juveniles is apparently greater than in that of adults. Variation in both juvenile growth rates and ages at maturity apparently causes most of the differences in body size of adults. Furthermore, a large portion of this variation may persist in the population, because growth rates among adults are low, and variation in growth rates of adults is not related to body size. Thus, the positive relationship between body size and age of sliders should be primarily considered an individual trait and only secondarily, if at all, a population trait. It follows then that indeterminant growth of an individual, operating through increased survivorship or increased reproduction associated with larger body size, should be viewed as a mechanism that may enhance natural selection for longevity by increasing the proportion of late versus early births of individuals. Therefore, we predict that indeterminant growth should be most prevalent in, but not an exclusive trait of, longer-lived species.

Theories of Life History Evolution

The papers of Fisher (1930), Svardson (1949), Cole (1954), Lack (1954a), and Williams (1957, 1966a,b) are examples of early contributions toward our understanding of the relationships between natural selection and life history traits. Over the past 20 years there have been many additions to the literature on life history evolution. The following is a partial list of contributions that are central to our current level of understanding of life history evolution: Lewontin (1958), Williams (1966a,b), Istock (1967), MacArthur and Wilson (1967), Murphy (1968), Tinkle (1969), Emlen (1970), Gadgil and Bossert (1970), Pianka (1970, 1972), Tinkle et al. (1970), Mertz (1971), Charnov and Schaffer (1973), Schaffer (1974a,b), Taylor

et al. (1974), Hirshfield and Tinkle (1975), Schaffer and Gadgil (1975), Nichols et al. (1976), Stearns (1976, 1977), Armstrong and Gilpin (1977), Case (1978), Maynard-Smith (1978), Whittaker and Goodman (1979), Charlesworth (1980), Stearns and Crandal (1981), Congdon et al. (1982), Goodman (1982), Lande (1982), Ballinger (1983), Caswell (1983), Dunham and Miles (1985), Stearns and Koella (1986). Many of these were certainly influenced by the original insights of Williams (1966a,b).

Two major selective factors have been explicated in most theories of life history evolution: resource availability (r- and K-selection—Dobzhansky, 1950; MacArthur and Wilson, 1967; Pianka, 1970, 1972) and the demographic environment or pattern of age-specific survivorship (demographic and bet-hedging theories—Williams, 1966a,b; Murphy, 1968; Stearns, 1976, 1977). Both theories attempt to predict whole suites of life history attributes based on a single selective factor, and attempts to test them have met with various results. Some problems associated with these attempts are that (1) there is a lack of sufficient data on life history traits and on environmental parameters such as resource levels (Stearns, 1976, 1977), (2) dramatically different selective forces may give rise to similar life history traits (Wilbur et al., 1974), and (3) most populations are not stable with respect to either resource levels or demographic environment.

The latter problem points out that for any life history study of animals to be successful, it must continue long enough to address the following issues. First, variation in life history traits among individuals within populations must be identified. An emphasis on variation among individuals represents a shift from traditional demographic studies on identifying the mean values of age-specific survivorship and reproduction. To identify variation among individuals, a mark-recapture study must continue long enough to follow individuals from early age classes to sexual maturity and beyond. A study of this nature on turtles is by definition long-term, because turtles do not mature early in life and are long-lived. Personnel, logistic, and funding problems associated with a long-term study are the primary reasons that most data on long-lived organisms are size-specific rather than age-specific. Miller (1976) made a cogent plea for the study of long-lived organisms, and Wilbur (1975a) stated that one of the most serious gaps in the study of life histories in general is the lack of data on long-lived iteroparous organisms. Weins (1977), Tinkle (1979), and Kephart and Arnold (1982) have emphasized the necessity of long-term studies that closely monitor populations while paying special attention to variation in individual and population attributes. Other notable contributions include the long-term studies of Tinkle (1967) and Dunham (1982) on lizards; Clutton-Brock et al. (1982) on red deer; Kephart and Arnold (1982) on snakes; and Stickel (1950, 1978), Gibbons et al. (1981, 1982), Gibbons (1982), and Congdon et al. (1983b,

1987) on turtles. Many of the chapters that follow should add to this foundation.

Hypotheses for Delayed Sexual Maturity and Iteroparity

Given the earlier statement that turtles are the paragons of delayed sexual maturity, longevity, and iteroparity (Wilbur and Morin, 1988), five evolutionary hypotheses warrant consideration:

1. Delayed maturity results in a gain in fecundity (Tinkle, 1969; Gadgil and Bossert, 1970; Wiley, 1974; Schaffer and Elson, 1975; Bell, 1977).
2. Delayed maturity results in an increase in survival of offspring (Hirshfield and Tinkle, 1975).
3. Delayed maturity results in a reduction in the cost of reproduction (*sensu lato* Tinkle, 1969).
4. Whether organisms mature early or late, iteroparity will be favored if adult survival rates are high relative to juvenile survival rates (Murdoch, 1966; Cody, 1971; Charnov and Schaffer, 1973).
5. Iteroparity will be favored if variation in the success of reproductive attempts is high (Holgate, 1967; Murphy, 1968; Stearns, 1976).

AGE AT MATURITY

The point at which a turtle reaches sexual maturity is probably an integration of sex, age, and body size. In addition, habitat quality and the nutritional state of turtles can affect the variation in age and body size at sexual maturity (Barney, 1922; Hildebrand, 1929; Parmenter, 1980; Gibbons et al., 1981). The models developed by Stearns and Crandal (1981) and Stearns and Koella (1986) demonstrate the need to identify the sources of variation of adult body size of females within a population and the relationship between age and body size at sexual maturity.

Among the smaller turtle species there is a strong correlation of the width of the pelvic canal opening and egg width (Tucker et al., 1978; Congdon and Tinkle, 1982a; Congdon et al., 1983a; Congdon and Gibbons, 1987). If pelvic aperture constrains the size of an egg that can be produced, this constraint may set the minimum size a female must attain to produce an egg large enough to contain sufficient material for embryogenesis and yolk reserves for the hatchling (Congdon, 1989; also see Chapter 8). Some support for this possibility can be found in the geographic comparisons of egg size in *Chrysemys picta* (Mitchell, 1985a).

Some confusion exists about the pattern of interaction of body size and age at sexual maturity among turtle species. It has been reported that sexual maturity is attained earlier in smaller species (Bury, 1979) and that age at

sexual maturity in turtles is not correlated with body size (Moll, 1979). Resolution of the conflicting reports about the relationships between age at maturity and body size will require additional data and careful analysis and may be confounded by the extreme interpopulation variation observed within some species (Gibbons et al., 1981). Males mature in many species at smaller sizes than do females, in other species at sizes similar to those of females, and in a few species at larger sizes than those of females (Bury, 1979). These different patterns in the sexes of body size at maturity are most likely related to mating tactics and territoriality of the species. *Trachemys scripta* mature at larger sizes in some tropical areas (Moll and Legler, 1971) than they do in temperate areas (Cagle, 1950; Gibbons, 1982). Gibbons et al. (1981) compared ages and sizes at maturity of males and females in thermally altered versus natural habitats. They concluded that male *T. scripta* mature at a fixed size regardless of age and that females mature at a fixed age regardless of size.

CLUTCH FREQUENCY

Clutch frequency in turtles has almost always been determined indirectly. Indirect methods commonly involve sampling adult females from a population and finding that the number of large ovarian follicles greatly exceeds the mean number of oviductal eggs, or that large follicles remain in the ovary even after one clutch is known to have been laid. A more direct determination comes from finding multiple sets of corpora lutea in the ovary (Cagle, 1950; Legler, 1960a; Powell, 1967; Gibbons, 1968d; Moll and Legler, 1971; Christiansen and Moll, 1973; Moll, 1973; Shealy, 1976). Ernst (1971b) and Moll (1973) correctly pointed out that no observed second clutches had been reported for *Chrysemys picta* until the early 1970s. Wilbur (1975) emphasized this void of data for Michigan populations, and other authors (Legler, 1954; Gemmill, 1970) have expressed doubts of second clutches (but see Snow, 1980, and Tinkle et al., 1981).

Gibbons (1982) presented data from a long-term study of three species of turtles in South Carolina, suggesting that in some cases clutch frequency may be a more important source of variation in annual fecundity than is clutch size. Until recently, determining clutch frequency for a population of freshwater turtles consisted primarily of demonstrating whether some individuals produced more than one clutch annually. Gibbons and Greene (1978) reported that, some adult *Deirochelys reticularia* might not reproduce every year. Since then, evidence that female turtles may skip reproduction some years has been reported for *Gopherus polyphemus* (Auffenberg and Iverson, 1979; Landers et al., 1980), *Chrysemys picta* (Tinkle et al., 1981), *Emydoidea blandingii* (Congdon et al., 1983b), and *Chelydra serpentina* (Obbard, 1983; Congdon et al., 1987).

Bull and Shine (1979) discussed the possible signifi-

cance and evolution of iteroparity, in which reproduction occurs in some individuals in the population every year but other individuals reproduce less often. They called this behavior "low frequency of reproduction" (LFR) and suggested that it would most often be found in animals incapable of producing more than one clutch per year and having some accessory activity associated with reproduction (e.g., breeding migrations, egg brooding, or bearing live young). The turtle species mentioned above exhibit no known accessory activity as defined by Bull and Shine (1979), and studies of *Chrysemys picta* (Tinkle et al., 1981), *Kinosternon subrubrum* (Gibbons, 1983), *D. reticularia* (Gibbons, 1969), and *T. scripta* (see Chapter 9) indicate that some individuals can produce two clutches per year. Some important goals of future research will be to identify the proximate causes of clutch frequency (Congdon and Tinkle, 1982a) and to clarify how age, age at maturity, and body size relate to the frequency that individuals in a population have second clutches or skip reproduction. These data are critical to testing models that relate fecundity to the evolution of age at maturity (hypotheses 1, 2, and 3) and to defining the type of iteroparity (clutch interval) that occurs in turtles (hypotheses 4 and 5).

CLUTCH SIZE AND FECUNDITY

An animal can increase immediate or annual fecundity in two ways: (1) by increasing clutch size with body size or age and (2) by increasing clutch frequency with body size or age. Lifetime fecundity can be increased by extending reproductive life without increasing annual fecundity. If larger body size of females is associated with increased age, then increased fecundity with age has often been demonstrated in reptiles as well as other organisms (hypothesis 1) through the positive correlation of larger clutch sizes with larger body sizes (Gibbons et al., 1982; Congdon and Gibbons, 1985). However, the assumption that body size and age are positively correlated in turtles has recently been questioned (see Indeterminant Growth, above).

EGG SIZE

Whereas a positive relationship of clutch size to body size frequently occurs in reptiles, a relationship between egg size and body size (or age?) occurs less often. Within most lizard species, clutch size, but not egg size, increases with body size (but see Stewart, 1979). However, in some species of turtles both clutch size and egg size increase with body size of females (hypotheses 1 and 2; *Chrysemys picta*—Congdon and Tinkle, 1982a; *Chelydra serpentina*—Congdon et al., 1987; *T. scripta*—Congdon and Gibbons, 1983). In no other species of turtles examined is the increase in egg size as pronounced as in *D. reticularia* (Congdon et al., 1983a; Congdon and Gibbons, 1987), in which

approximately 75% of the increase in clutch mass associated with increased body size results from increased egg size. Egg size has been shown to be positively related to body size of hatchlings (Congdon et al., 1983a; also see Chapter 8). Although it has not been documented, larger hatchlings are believed to have higher survivorship than do smaller hatchlings. Therefore, increased egg size should be viewed as a mechanism by which animals with indeterminate growth can increase the quality of their offspring that are produced later in life. The relationship of egg or offspring size to body size and age must be well documented to test hypothesis 2. In addition, data on the relationships among egg size, clutch size, body size, age at sexual maturity, and age of reproductive adults are necessary to determine if there are interactions among the benefits proposed in hypotheses 1 and 2.

The development of hypotheses 3, 4, and, by logical extension, 5 can generally be traced to the attempt by Cole (1954) to discover how great an increase in fitness (defined as r) is caused by reproducing more than once (iteroparity) rather than only once (semelparity) in a lifetime. In Cole's model the population age structure was assumed to be stable, and there was no mortality except that semelparous organisms died immediately after reproduction (i.e., the value of r depends on fecundity and age at maturity only). Murdoch (1966) criticized Cole's result as being too simplified. Gadgil and Bossert (1970) assumed that there was juvenile but no adult mortality, whereas Bryant (1971) assumed that adult and juvenile mortalities were equal. Charnov and Schaffer (1973) compared annual and perennial populations and emphasized the importance of keeping mortality of juveniles and adults separate. They concluded that the absolute gain in intrinsic population growth rate achieved by iteroparity was equivalent to adding to the average clutch size the number of individuals that is equal to the ratio of adult mortality rate to juvenile mortality rate. Thus, they predicted that iteroparity would be favored when adult survivorship is high relative to that of juveniles (hypothesis 4). Holgate (1967) and Murphy (1968) pointed out the problems an organism faces when juvenile mortality is highly variable and when there is a high probability that any given reproductive event may result in total failure (hypothesis 4).

SURVIVORSHIP AND LONGEVITY

Two studies have documented nest survivorship in freshwater turtles over six years in *Emydoidea blandingii* and over eight years in *Chelydra serpentina* (Congdon et al., 1983b, 1987). Nest mortality in Blanding's turtles ranged from 42% to 93%, with a mean of 67%, and in snapping turtles it ranged from 30% to 100%, with a mean of 70%. The primary predators of nests of both species are raccoons (*Procyon lotor*) and red foxes (*Vulpes vulpes*). Adults of both

species of turtles are seldom harmed by either predator.

Mortality rates of juvenile turtles are poorly known, despite their importance in population dynamics (Wilbur and Morin, 1988). Cumulative survivorship of a cohort of 125 *T. scripta* hatchlings to age 4 was 0.18; however, the majority of the mortality occurred between hatching and the end of the first year in the aquatic habitat (see Chapter 15).

Survivorship of adult turtles in most cases is high. Reports of annual survivorship include *Chelydra serpentina*, .93 to .97 (Galbraith and Brooks, 1987); *Chrysemys picta*, .76 to .83 (Wilbur, 1975a); *Geochelone gigantea*, .84 to .98 (Swingland and Lessells, 1979); *Terrapene carolina*, .85 to .94 (Stickel, 1978; Williams and Parker, 1987); *T. ornata*, .78 (Blair, 1976, in Wilbur and Morin, 1988); *Trachemys scripta*, .81 to .84 (see Chapter 15); and *Xerobates agassizii*, .98 (Turner and Berry, 1986). Although these survivorship rates are remarkable, it has been pointed out that even with annual survival rates of 90%, only 1 in 100 turtles would be alive after 44 years (Wilbur and Morin, 1988).

Although data on the relative survivorship of adults and juveniles are scarce, mortality rates of embryos in the nest and of first-year hatchlings are apparently much higher and more variable than those of adults (*Chrysemys picta*—Tinkle et al., 1981, and Wilbur, 1975a; *E. blandingii* and *Chelydra serpentina*—Congdon et al., 1983b, 1987; *T. scripta*—see Chapter 15). Thus, it appears that mortality of eggs, embryos, and juveniles is high relative to that of adults (hypothesis 4), and in the case of eggs and embryos mortality is probably more variable (hypothesis 5).

Little data exist on the longevity of turtles and on the survivorship of various age classes. Gibbons and Semlitsch (1982) have estimated that *Trachemys scripta* live to approximately 30 years of age, and individuals greater than 30 years old have been documented for populations of *Terrapene carolina* (Oliver, 1955; Stickel, 1978) and *T. ornata* (Blair, 1976). Data from the study by Woodbury and Hardy (1948) of the desert tortoise (*X. agassizii*) and past studies of Blanding's turtles (*E. blandingii*) on the E. S. George Reserve (Sexton, 1959a,b; Wilbur, 1975a,b; Congdon et al., 1983b) indicate that longevity may exceed 60 years in nature.

Because these studies clearly document that turtles can live a long time, it is appropriate to ask whether there is any substantive evidence for senescence in turtles. Moll (1979) and Dunham et al. (1988a) cite reports of senescence in three species of turtles: *Deirochelys reticularia* (Gibbons, 1969), *Terrapene ornata* (Legler, 1960a), and *Trachemys scripta* (Cagle, 1946). Cagle (1944c) examined 183 female *T. scripta* ranging from 70 to 260 mm in plastron length that had follicles greater or equal to 15 mm in diameter, and 138 females from 70 to 230 mm in plastron length that had follicles less than 15 mm in diameter. Cagle (1944c) stated: "It has been commonly assumed

that fishes and reptiles remain reproductively active throughout their lives. The repeated observation of senile turtles has indicated that this is not true for the species considered here. Of 183 females examined, 7, ranging in size from 210 to 220 mm. and apparently of great age, contained senile ovaries." No explanation of the criteria used to make this assumption was given. Gibbons (1969) stated: "The absence of enlarged follicles in four of the five specimens [of *D. reticularia*] greater than 180 mm suggests the possibility of senility or a reduced reproductive rate in older individuals." However, it should be noted that a later assessment (Gibbons and Greene, 1978) based on an additional decade's worth of data and the use of x-radiography was that some females were not reproductively active in some years but were in subsequent ones. Legler (1960a) stated that for *Terrapene ornata* "one ovary may become senile in old females before its partner does; this may explain the occasional absence or atrophy of one ovary in large females that I have examined." Cagle, Gibbons, and Legler apparently assumed that size and age are correlated, an assumption that has been questioned in an analysis of *Trachemys scripta* (Gibbons, 1982). We conclude that in each of the above cases there was no compelling reason to evoke senescence as the cause of the absence of reproduction in a turtle in a given year.

Summary

A life history is a suite of coevolved characteristics that directly influence population parameters. Because turtles are among the longest-lived vertebrates, concepts related to senescence are of obvious interest because they may have had substantial impact on life history evolution. Two evolutionary theories of senescence—mutation accumulation and antagonistic pleiotropy—were examined for aspects that seemed important to life histories. Factors, such as age at death and indeterminate growth, that influence the ratio of early births to late births by females appear to be critical to the evolution of longevity. A positive correlation between age at maturity and estimates of longevity among species would appear to be more consistent with the antagonistic pleiotropy theory than with the mutation accumulation theory. However, both processes may play a role in determining the absolute life span of individuals. The protective shell, which has been present in fossil turtles since the Triassic period, about 200 million years ago, appears to have played a central role in allowing turtles to evolve longevity by (1) decreasing adult deaths due to extrinsic causes, (2) increasing the proportion of late births relative to early births, (3) allowing more adults to live long enough for senescence traits to become implicated in their deaths, and (4) permitting natural selection to act on age-of-onset modifiers, and suppression genes to act on traits of senescence. Indeterminate growth may also have been an important mecha-

nism allowing older, and thus larger, turtles to increase their reproductive output and, for some species, the quality of their offspring. However, variation in reproductive characteristics of *T. scripta* is more strongly correlated with body size than with age. Because body size plays an important role in determining the annual and lifetime reproductive output of turtles, and because age is implicated in almost all theories of life history evolution, the cause of the apparent discrepancy between individual and population traits in some turtles needs investigation.

At present, theories (r- and K-selection, demographic, and bet-hedging) that attempt to predict associations of life history characteristics based on a single selective factor have not been notably successful. More-specific theories that attempt to predict the direction of selection on a single trait (such as age at sexual maturity, iteroparity, or quality of young) seem to hold more promise. Turtles appear to have many traits that make them good models for tests of these theories:

1. Turtles can be individually marked, and the mark is relatively permanent throughout their lives.
2. They occur at population densities that provide adequate numbers of marked individuals and are still manageable in field situations.
3. For many species, early ages can be determined from growth rings laid down in their shells.
4. Turtles reproduce more than once in their lifetimes, and some reproduce more than once in a single season.
5. Both clutch size and egg size increase with body size in some species.
6. All turtles produce eggs with calcified shells that allow their reproductive output to be determined non-destructively and repeatedly by x-radiography.

Recent advances in the area of ultrasound tomography, telemetry, and the use of lipid-soluble gases to determine whole-body lipid levels should help answer questions about age-specific resource allocation patterns that are important in understanding life histories.

Many estimates of survivorship of adults are greater than .90, and some estimates are as high as .97. Even with survivorships of .90, only 1 in 100 turtles would be alive after 44 years. Reliable records of turtles living more than 60 years in the wild indicate that adult survivorships are indeed that high or higher. For some species, reproductive life span may exceed 30 years; however, there are apparently no convincing data that reproductive senility occurs in turtles. Several factors make it extremely difficult to collect reliable evidence for senility in turtles. First, even with high adult survivorships, few very old individuals will exist in a population, so the potential source of data is low. Second, turtles are not social animals, so they cannot affect the fitness of their offspring after the first

year of life. Therefore, natural selection should favor postponement of senescence in an individual only during its reproductive life, and reproductive failure and death should be closely linked in time. Third, variability in clutch size and clutch frequency due to proximate causes such as resource availability would affect all age groups and, because the number of old individuals is small, might mask variations in reproductive parameters that are due to senescence.

We believe that long-term field research documenting variation in life history characteristics of turtles both within and among individuals will continue to provide new insights into life history processes of long-lived organisms. Such insights can become the basis for tests of current life history theories and will eventually lead to the develop-

ment of new theories based on a more comprehensive understanding of life history processes.

Acknowledgments

We thank the following individuals for comments and discussions that improved early drafts of this manuscript: John Aho, Roger Anderson, Robert Fischer, Trip Lamb, and David Scott. Research and manuscript preparation were aided by National Science Foundation grants DEB-79-06031 and BSR-84-00861 to Justin D. Congdon and DEB-79-04758 to J. Whitfield Gibbons, as well as contract DE-AC09-76SROO-819 between the University of Georgia and the U.S. Department of Energy.