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# SURVIVORSHIP AND LONGEVITY OF A LONG-LIVED VERTEBRATE SPECIES: HOW LONG DO TURTLES LIVE?

BY J. WHITFIELD GIBBONS AND RAYMOND D. SEMLITSCH
*Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29801 U.S.A.*

## SUMMARY

(1) A 13-year mark-release-recapture study on natural populations of freshwater turtles, *Pseudemys scripta*, of known age indicates that approximately 1% of the individuals can be expected to attain an age of 20 years.

(2) Probable maximum longevity in natural populations is about 30 years, in contrast to published estimates of up to 75 years.

(3) Adults follow a Type II survivorship curve with constant rates of mortality at all ages, as do many other long-lived species that have been studied.

## INTRODUCTION

In the study of natural populations of animals, the survivorship pattern is a critical life history attribute but is difficult to determine. Many theoretical life history models depend upon whether a species is short-lived or long-lived (Tinkle 1969; Stearns 1976); therefore, quantitative assessments of age structure, survivorship, and longevity are essential to certain life history concepts.

Determinations of maximum longevity have been made for many species because of the ease by which lifespan can be recorded in individuals under certain circumstances, such as in zoos. In a comparison of more than 700 species of vertebrates representing all major classes, turtles and crocodilians were unquestionably the longest-lived (Gibbons 1976). Maximum longevity under zoo or laboratory conditions may reflect comparative age structures and survivorship patterns, but the relationship between them is known in few natural populations, particularly those of long-lived species.

Age structure and survivorship patterns have been accurately determined in short-lived species of lizards (Tinkle 1967; Dunham 1978) and some that live for 5–9 years (Zweifel & Lowe 1966; Tinkle & Ballinger 1972). This is relatively short compared to turtles, many species of which do not reach maturity before 5 years of age (Tinkle 1961; Gibbons 1968; Ernst & Barbour 1972; Wilbur 1975; Swingland 1977; Gibbons *et al.* 1981; Tinkle, Congdon & Rosen 1981). Individual captive (Gibbons 1976) and, on occasion, wild-caught turtles (Schneck 1886; Blair 1976; Stickel 1978) have been documented to live more than 50 years.

Although longevities are impressive for some turtles (Blair 1976), overall survivorship pattern is difficult to establish for these, or other animals because of the difficulty of verifying the age of individuals that pre-date the study. Growth annuli (Deevey 1947; Jones 1981) can be used effectively with some turtles (Sexton 1959). Our objective is to document the general pattern of survivorship and longevity in a freshwater turtle and to compare the results with reports for other long-lived animals. Our findings are based on long-term studies of turtles whose age was determined by the use of growth annuli and the mark-release-recapture technique.

Few studies have lasted long enough to estimate with confidence the maximum longevities of a significant portion of a natural population of turtles (Woodbury & Hardy 1948; Legler 1960; Wilbur 1975; Blair 1976; Stickel 1978). In *Pseudemys scripta* (Schoepff), examined by us, previous investigators have estimated that individuals in natural populations may attain ages from 30 (Moll & Legler 1971) to 75 years (Cagle 1950). Individuals in the closely related *Chrysemys picta* have been estimated to reach 40 years of age (Gibbons 1968; Wilbur 1975). We provide evidence of maximum longevity and the survivorship pattern of the slider turtle, *P. scripta*, based on 13 years of data from South Carolina populations.

## METHODS

Mark-release-recapture studies began in aquatic habitats (Gibbons & Patterson 1978) on the U.S. Department of Energy's Savannah River Plant near Aiken, South Carolina, U.S.A., in July, 1967, and continued to the present. During this period 2888 *P. scripta* have been individually marked and 2204 subsequently recaptured. Turtles were collected by a variety of means over the study period, but the majority were captured in aquatic hoop traps or by terrestrial drift fences and pitfall traps (Gibbons 1970). Certain critical records were obtained by finding the shells of dead, marked individuals during frequent searches in areas peripheral to aquatic study sites.

A variety of standard measurements (Gibbons 1969) were taken on each live individual or shell including age, when possible, using the annuli method (Sexton 1959) and plastron length. Therefore age could be determined in older, recaptured individuals without discernible annuli if they had been accurately aged as juveniles.

The most intensive field studies were conducted in Ellenton Bay, a natural freshwater habitat and a typical Carolina bay. Carolina bays are a regional, unexplained geological phenomenon occurring throughout much of the southern Atlantic Coastal Plain and represent the dominant lentic habitat for semi-aquatic vertebrates, including freshwater turtles. Carolina bays vary in size but are always ovate in shape with the long axis oriented northwest-southeast. They characteristically have no tributary water supply so that water level is dependent exclusively upon precipitation and evaporation. Consequently annual variations in rainfall at Ellenton Bay have resulted in an aquatic habitat ranging from fewer than 100 $m^2$ of shallow (<20 cm) open water (in 1968 and 1981) to an aquatic area more than 10 ha and 1·5 m in depth (in 1977).

Despite the natural variation in the aquatic environment, Ellenton Bay has supported populations of six species of aquatic turtles (Gibbons 1970) throughout the 13 years of study. An indication of fidelity to the particular site is that each species has individuals which were marked initially in 1967–1968 and recaptured in 1980–1981. The turtle species consistently having the largest population size at Ellenton Bay is *P. scripta*. Because the Savannah River Plant is a restricted access area for security reasons, the turtle populations at Ellenton Bay receive minimal impact from human interference or industrial, agricultural, or urban activities.

The regional climate is warm temperate with a mean air temperature of 80 °F (27 °C) in July. Winter (January) mean air temperature is 46 °F (8 °C). Mean annual rainfall is 43 inches (1·8 m).

## RESULTS

A survivorship curve was constructed from 560 known-age *P. scripta* inhabiting Ellenton Bay. The curve represents a minimal estimate because each point represents the last capture of an individual and not necessarily its death. At the last capture it was assumed the individual was present during each previous age class. All biases inherent in this approach tended to result in underestimates of survivorship since the higher age classes are only represented by recaptures of animals aged by annuli when younger. The increasing ineffectiveness of the annuli method at higher ages and consequent dependence upon recapture, leads to mortality rates in the older age classes being overestimated. Long-term recapture records of all known-age individuals from other populations on the Savannah River Plant were also considered, to obtain estimates of maximum longevities.

Survivorship of *P. scripta* approximates a Type II survivorship curve (Pearl 1928), in which mortality remains at a constant rate at all ages (Fig. 1). Based on the minimal survivorship estimate, only 10% of a population lives for a decade and only 1% of the individuals reach ages greater than 20 years. Maximum longevity would be approximately 30 years (Fig. 1).

Of thirty-two turtles recaptured after 10–13 years, eight had been too old upon initial capture to be reliably aged by annuli. The elimination of these individuals from calculation

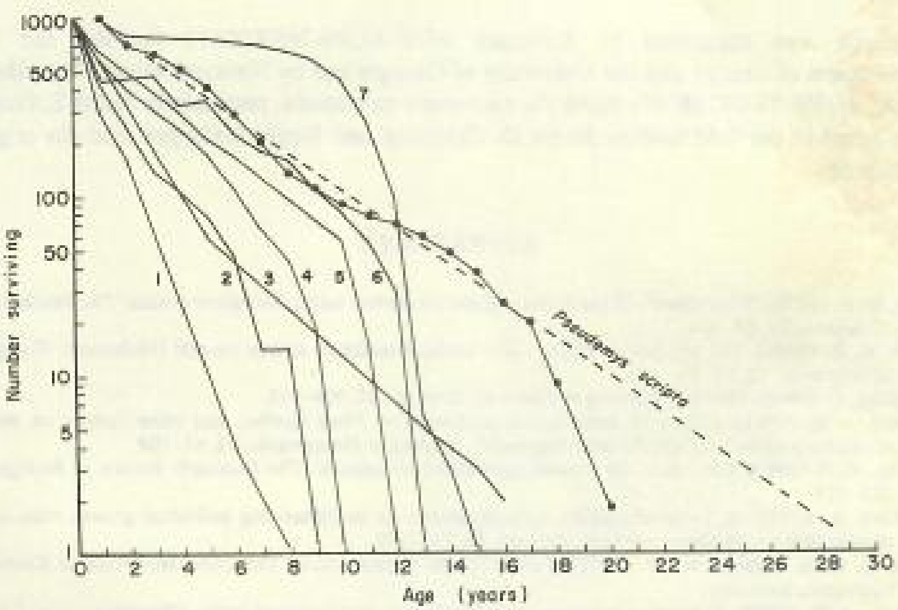


FIG. 1. Survivorship curve (unbroken line and dots) for 560 known-age *Pseudemys scripta* from Ellenton Bay in South Carolina compared to those of other long-lived species in natural populations. The dashed line for *P. scripta* represents a calculated survivorship curve based on the data from individuals 1–15 years of age ($\log \hat{Y} = 3{\cdot}071 - 0{\cdot}103X$). The numbers indicate references for survivorship curves of natural populations of other species as follows: (1) *Sceloporus virgatus* (lizard); Vinegar (1975); (2) *Balanus glandula* (barnacle); Connell (1961); (3) *Desmognathus ochrophaeus* (salamander); Tilley (1980); (4) *Larus argentatus* (bird); Paynter (1947); (5) *Chrysemys picta* (turtle); Tinkle *et al.* (1981); (6) *Hemitragus jemlahicus* (mammal); Caughley (1966); (7) *Ovis dalli* (mammal); Deevey (1947).

of the survivorship curve (Fig. 1) results in a bias of overestimating mortality in the older age classes. The ages of these individuals can be approximated from their size at initial capture and from the adult growth rates of *P. scripta* in this population (Gibbons *et al.* 1981). Even using this procedure, the oldest turtles were estimated to be less than 35 years old at the time of last capture. No known-age specimens from other populations exceeded 30 years.

## CONCLUSIONS

We conclude that the survivorship curve with the projected estimate for older animals (Fig. 1) is a realistic model of longevity for this species. We further conclude that although individual turtles held captive in protected situations can be expected to attain old ages the survivorship pattern in natural populations of these and other animals groups will reveal that the majority of the members of natural populations have much shorter lifespans than that promoted by popular conception. Furthermore, although turtles are indeed suitable representatives of long-lived species in population studies, long-term research programs (Tinkle 1979) are necessary to reveal the survivorship pattern of this or any other group in a quantitative manner.

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