

# *Introduction*

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## The Slider Turtle

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### Abstract

A general overview is given of the systematic status and natural history of the slider turtle, *Trachemys scripta*.

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### Introduction

In Charleston, South Carolina, the year 1855 was a notable one, although the significance of particular events depended—as it does today—on where your interests lay. For politicians, a significant issue was the recent passage of the Kansas-Nebraska Act, which opened settlement of the two territories to both slave owners and non-slave owners. For those interested in the military defense of the city, a key concern was the condition of Fort Sumter, a small facility in Charleston Harbor. But for people who were interested in natural history, the capture of a particular turtle near the city would mark an altogether different beginning. The ultimate significance was that the specimen that Louis Agassiz had captured would later be cataloged under the name of *Emys serrata* as the first reptile entered into the vertebrate collections of the newly formed U.S. National Museum in Washington, D.C. Its nomenclature would change over the years from *Emys serrata* to *Trachemys scripta* to *Pseudemys scripta* to *Chrysemys scripta*, depending upon the year and the turtle biologist who was using the name. The specimen, which now resides in a jar of alcohol in the support center of the Smithsonian Institution, is a slider turtle, the subject of this book.

A basic question in the study of an animal or plant species is, Why does the species function in the manner in which it does, rather than in some other way? This question can be formulated at all levels, from the precise physiological, morphological, or genetic questions to the more complex questions of why it has a certain behavior pattern

or community association. However the question is posed, some of the first answers required are how the organism performs biologically, how it is structured, and where it lives.

In the thinking of some scientists the idyllic study in ecology is a project undertaken to address a theoretical question that is recognized as being of current interest and that has been posed in order to satisfy or refute a model. The study organisms are used simply to test the model and provide generalities that can then be broadly applied, thus eliminating the need for detailed observation of each species. However, no matter how esoteric a model or how theoretical a question is, the final answers must come from empirical evidence emanating from the examination of particular species—their habits, morphology, physiology, genetics, behavior, and community relationships.

Another approach is to begin investigation of the ecology of a species with the objective of unraveling and understanding as much of its natural history as possible. A common approach with studies of this nature is to use the findings later to test a theoretical question or model. This is frowned upon as the ideal, but its widespread use bespeaks its practicality. Yet another approach in scientific writing for those interested in theoretical questions is to use earlier presentations of basic ecological information on a species that are appropriate for testing the model or addressing the theoretical question.

The information presented in this book is a mixture of approaches, including the last, in that it should provide information that may later be used by others. I do not pass judgment on which is the best approach to science, but I do maintain that our fundamental question is to understand how animal and plant species function; that is, Why are they the way they are? Any information that can contribute toward this understanding is, in my opinion, useful and should not be belittled.

The objective of this work is to use the ecological observations on the turtles of a selected geographic region in order to understand the natural history of the species as thoroughly as possible. The life history features of common freshwater turtles in selected populations have been examined by ecologists on the Savannah River Plant (SRP) in South Carolina since 1967 (Appendix 1.1). By far the most ubiquitous and abundant of these turtles is the slider, *Trachemys scripta*. These studies on the SRP have been augmented by the research of others on slider turtles in the same or other regions. I hope that collectively the research presentations will be revealing of the life history, ecology, and evolution of the slider turtle as well as of turtles as a group. These findings, or any hypotheses generated from this information, should allow us to address some of the basic questions posed by ecologists about how the world's environments and attendant organisms function.

## Turtle Populations

In the study of turtles, countless questions may be asked about individuals, populations, or species and why they function in the way they do. The individual is accepted as the primary unit of selection, and although no one has difficulty defining what an individual turtle is, the individual's characteristics that are subject to natural selection may be difficult to ascertain. At the next level, the population, where the overall expression of selection is observed, a definition of the unit of study itself can present problems. How are the populations of a species of turtle in a region defined and demarcated? Which individuals are included in the population?

Among the variously stated definitions of a population is the classic one that a population is a group of individuals that intermix genetically with other members of the group more so than they do with similar neighboring groups. In my early studies of turtle populations, I often declared that some species of freshwater turtles were ideal for population studies because they occurred in circumscribed bodies of water (e.g., lakes), so that the population was an identifiable unit. Several thousand marked turtles later, I concluded that this is a fallacy. Exchange among individuals from neighboring habitats is commonplace, and such well-defined genetic populations seldom exist, or at least have not been identified empirically.

The population concept as applied to turtles, and most other animals, must be viewed as a continuum ranging from groups of individuals that fit the true population model (having practically 100% genetic mixing with no outside interlopers or interloping) to the other extreme, in which gene flow is panmictic over a large region. Defining the boundaries of a population may be confounded by discovery of areas where turtles congregate for winter dormancy or for summer feeding and that include individuals from a variety of different genetic units. I do not have evidence of this phenomenon, but it is certainly conceivable, considering the complexity of behavior and population structure that is being revealed in turtle populations.

But to do population studies, one must define the population, and with freshwater turtles this is not easy. After coming full circle, I would once again define a freshwater turtle study population in terms of the body (and nearby bodies) of water that a group of individuals inhabit. So the term "population" becomes the word of convenience when referring to groups of animals that live in an area (defined as the study area) and intermix genetically. It must be understood in the use of this term that some populations are more tightly structured genetically than others. That is, gene flow has at least some probability of occurrence even in the most remote populations as long as there are other populations of the species in existence. The critical factor becomes the establishment and definition of

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the study area, as that will be what the investigator must use in defining the population.

My studies with turtles have led me to the belief that populations, however defined, and our expressions of them (such as population structure, life tables, and survivorship curves) are consequences of a variety of temporal and spatial stochastic events. Although a particular population of turtles may be quantified in terms of population parameters, the specific quantification will be applicable only to the group of individuals at the particular time and place but not necessarily to groups of individuals in other places or to those in that place at another time. Thus, the defining of population characteristics must be viewed with caution in terms of their applicability to the species. A comparison of population parameters of different populations of the slider turtle will make this point in various chapters of the book. In essence, each individual is operating only to increase its own fitness, and its mode of operation will vary to fit the local demographic and environmental conditions to which it is subjected.

Our general conclusions about population dynamics of turtles may be far more limited than we presently believe. In short, populations are merely assemblages of individuals of a species as we perceive them, and they have few inherent properties that are consistent across different populations. Furthermore, I believe that if this concept of population is critically examined for most species of animals or plants, the same will be able to be said. That is, populations of a species cannot be depended upon for consistency but are based only on the stochastic history of the individuals that constitute them.

### The Study Species

The pond slider (*Trachemys scripta*) has one of the more extensive geographic ranges of the vertebrate species in the Western Hemisphere and has numerous subspecies, some of which are contested to be true species. The subspecies-species controversy notwithstanding, the yellow-bellied slider turtle is generally accepted as a subspecies of *Trachemys scripta* that inhabits the eastern United States. The populations on the SRP in South Carolina belong to the subspecies *T. s. scripta*.

The questionable phylogenetic relationships of the slider turtle and related species have led to taxonomic confusion about the genus or genera to which these species belong. This confusion is evident in the fact that this species has been referred to in the refereed scientific literature by three different generic names (*Pseudemys*, *Chrysemys*, *Trachemys*) in a single decade (Table 1.1). For purposes of the present writing, it should be understood that a single species, or even subspecies if one wishes to drop to that level, occurs within the geographic range of the samples from South Carolina. I believe everyone would agree

Table 1.1. Brief chronological summary of selected classification schemes proposed for the *Chrysemys/Pseudemys/Trachemys* complex

Reference	<i>Chrysemys</i> ( <i>picta</i> )	<i>Pseudemys</i>	<i>Trachemys</i> ( <i>scripta</i> )
Agassiz (1857)	C	P	T
Cope (1875)	C	P	P
Boulenger (1889)	C	C	C
Carr (1952)	C	P	P
Conant (1958)	C	P	P
McDowell (1964)	C	C	C
Zug (1966)	C	P	T
Weaver and Rose (1967)	C	C	C
Parsons (1968)	C	C	C
Ernst and Barbour (1972)	C	C	C
Conant (1975)	C	C	C
Ernst and Ernst (1980)	C	P	P
Vogt and McCoy (1980)	C	P	P
Seidel and Inchaustegui Miranda (1984)	C	P	T
Ward (1984)	C	P	T
Obst (1985)	C	C	C
Iverson (1986)	C	P	T
Seidel and Smith (1986)	C	P	T

Note: Taxonomic designations are those of Seidel and Smith (1986), in which *Chrysemys* contains only *C. picta*, *Trachemys* contains *T. scripta* and the West Indian species of slider turtles (Iverson, 1986), and *Pseudemys* contains all other members of the complex. The generic recognition of each taxon by an author is indicated by its first letter.

\*The taxonomic designations of Seidel and Smith (1986) for the species are allocated to subgeneric status under the genus *Chrysemys*.

about that. What people do not agree about is the phylogenetic status of this species relative to closely related species. All authorities, to my knowledge, also agree that the genus that includes slider turtles, no matter which species are included, is restricted to the Western Hemisphere, except for modern introductions elsewhere.

A difficult decision for me in considering the preparation of this book was whether to allow authors to use the genus name of their choice or to recommend strongly that they use a particular one in order to standardize the presentation. The dilemma was of course whether to confront turtle researchers whose foundation in systematics far exceeded my own. In the end, the choice was not a difficult one for me. I elected to use *Trachemys* and make my choice known to the other contributors whose manuscripts arrived using the names *Trachemys*, *Pseudemys*, and even *Chrysemys*. Contributors then used the name that they preferred without the requirement that justification be given.

From the viewpoint of an ecologist, the role of a name is to identify what you are talking about. This is the important feature in the study of a species as a functional unit in an ecosystem. The significance of the name of an organism from the standpoint of the systematist can be based on either of two issues. The first is the assessment and interpretation of the phylogenetic relationship of the species to other members of the genus or to closely related genera. This issue is often shrouded in opinion, and because inter-

Table 1.2. Nomenclatural origins of names of the slider turtle

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emys—Gr. <i>emys</i> , genit. <i>emydos</i> , a freshwater tortoise
pseud—Gr. <i>pseudēs</i> , false, deceptive
script—L. <i>scriptus</i> , written, p.p. of <i>scribo</i> , to write
chrys—Gr. <i>chryso</i> , gold
trachy—Gr. <i>trachys</i> , rough

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Source: Jaeger, 1944.

pretive science is not a democratic process, we have no jury processes for indictment and conviction. The second issue is etymological and often comes down to the rather basic process of which letters of the alphabet are used. Biologists have built careers and fed their families through addressing these two issues, especially the former, with their chosen organisms. In fact, the slider turtle may have fed more people, in this indirect manner, than any other North American turtle. An accounting of what the slider turtle has been called generically during the last 130 years is presented in Table 1.1. Figure 1.1 indicates the geographic ranges of the various North American species that are or have been included in the same genus as *T. scripta*, under the names *Pseudemys* or *Chrysemys*.

### Taxonomic Pronunciation

As best as I can tell, the slider turtle is indeed among the front-runners in the number of accepted generic epithets that have been used in the last decade. Of equal interest are the numerous pronunciations that have been used for each of the generic names. The word *emys* is Greek and means turtle. All of the genus names thus have been of Greek origin (Table 1.2), whereas *scripta* is from Latin.

I have heard *Pseudemys* pronounced as 'süd ə mēz, süd 'em ēz, süd 'em es, and even süd 'ē mis (diacritical marks are those used in *Webster's Ninth New Collegiate Dictionary*). *Chrysemys* has been pronounced by reputable turtle biologists I have known as 'kri sə mēz, 'kris ə mēz, kri 'sem es, kris 'em ēz, and even kris 'sēm es. *Trachemys* is a new one for most of us, and so far I have heard it called only 'trāk ə mēz, 'trak ə mēz, and trak 'em es. I am sure we need only a little more time with this one.

Ernst and Barbour (1972) offer cry'-sē-mēz ('kri sə mēz) as the proper pronunciation of *Chrysemys* and do not give pronunciations for *Pseudemys* or *Trachemys*. So far, I think everyone agrees that *scripta* is pronounced skript'-a, as in Ernst and Barbour (1972).

### Natural History of the Slider Turtle

Several excellent accounts have been given of the life history, ecology, and behavior of the slider turtle in general works (Carr, 1952; Ernst and Barbour, 1972) and monographs on the species (Cagle, 1950; Moll and Legler,

1971). Perhaps the greatest number of turtle ecology studies have been on the closely related painted turtle *Chrysemys picta* (Cagle, 1954; Sexton, 1959b; Gibbons, 1967b, 1968c,d; Ernst, 1971c,d; Wilbur, 1975a; and others), and they augment our understanding, although most were conducted in colder temperate areas outside the range of *T. scripta*.

*Trachemys scripta* is a semiaquatic species in which individuals remain in aquatic areas, generally where submerged and floating vegetation is heavy, except for terrestrial excursions, which have several readily identifiable purposes that include travel of hatchlings overland from a terrestrial nest to water, travel by the female to a nesting site, movement to and from hibernation sites or alternate feeding areas, departure from an unsuitable habitat (Cagle, 1944b; Gibbons et al., 1983; Parker, 1984), and travel by males in search of females (Morreale et al., 1984). The basking habit is well noted in all species of the group, and a significant portion of time is spent in absorbing sunlight on the bank or protruding objects or in basking aquatically (see Chapter 22).

The basic life cycle of the species in temperate regions is one in which eggs are laid in early spring in an underground nest dug by the female, with the young hatching in about three months. The hatchlings usually remain in the nest cavity for the duration of fall and winter (Gibbons and Nelson, 1978). Upon emergence in early to late spring, the hatchlings enter the aquatic habitat and begin feeding, approximately one year after being deposited as eggs. The juveniles are preferential carnivores (Clark and Gibbons, 1969), as are the adults when a high-protein diet is available (Parmenter, 1980). Individuals can subsist on a vegetative diet, although growth rates may be significantly slower than in populations in which individuals have carnivorous diets.

Growth rates are influential in the attainment of maturity in that males in a region tend to reach maturity at a set size range whereas females reach maturity more as a function of age (Gibbons et al., 1981). Therefore, males in a population of fast-growing turtles tend to reach maturity at a younger age, and females at a larger size, than those in a population of slow-growing individuals. However, it should be stated that the age-size relationships to maturity in the sexes are highly complex and await further detailed studies to refine our understanding of them.

Sexual dimorphism is apparent in foreclaw length and tail length (both significantly longer in adult males than in females) and in the much smaller size of males than females within a geographic region. Geographic variation is evident in that both sexes of this species from Panama (Moll and Legler, 1971) are dramatically larger than those in the United States (Conant, 1975). However, variation in size can be significant among populations within a geographic region, as is evidenced by the much larger size of slider turtles in the Par Pond Reservoir (which

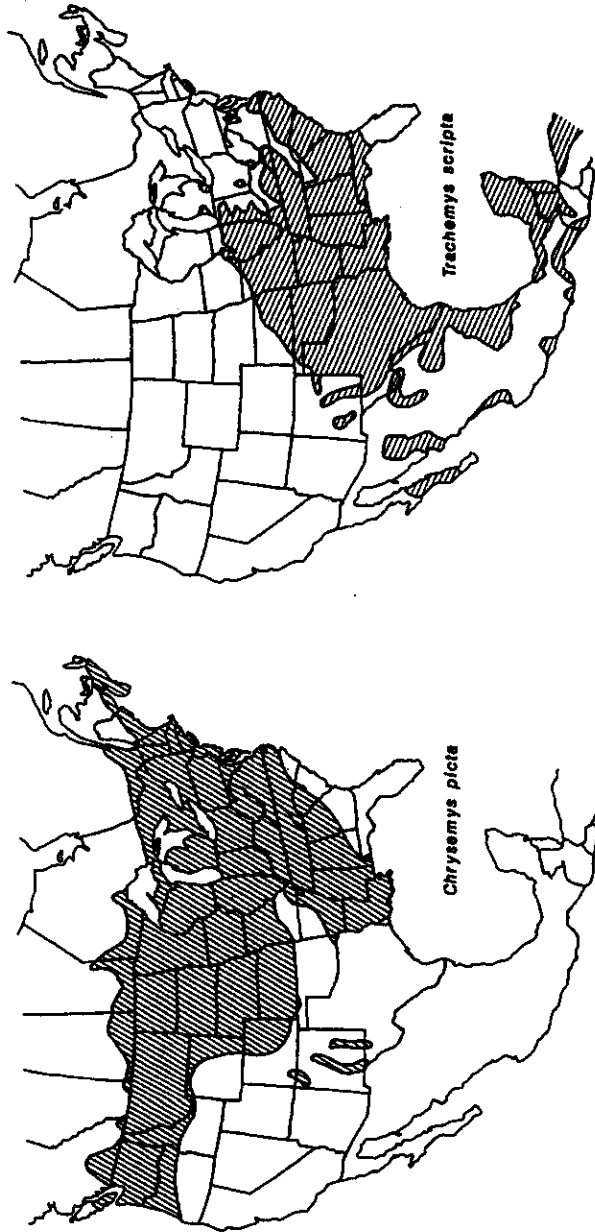
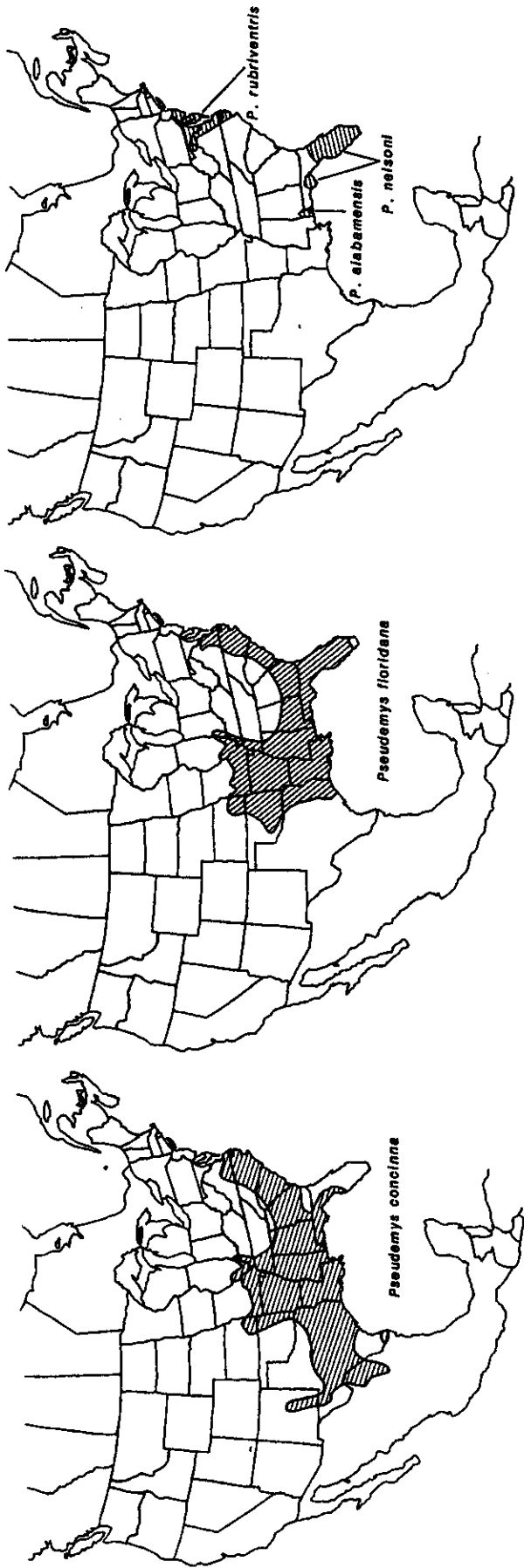


FIGURE 1.1. Geographic ranges of North American species of turtles that have been included in the same genus (*Pseudemys*, *Chrysemys*, or *Trachemys*) as the slider turtle during the last 10 years. Genus and species epithets are those currently accepted by Seidel and Smith (1986). Geographic ranges are based on those given by Conant (1975).

receives thermal effluent from a nuclear reactor) than of the natural population at Ellenton Bay less than 20 km away (Gibbons, 1970d). Also, individuals in some tropical populations are not larger than those in typical temperate populations. Geographical variation in body size is another issue that is in no way resolved.

Mating occurs in the spring, although courtship behavior by males has been observed in both fall and winter and may occur to some degree year-round. Observations of slider turtles in the tropics suggests that they are reproductively active from early fall to spring (Moll and Legler, 1971). Females presumably retain viable sperm for many months, as is reported for other turtles (for a review, see Ehrhart, 1982), so the timing of copulation relative to ovulation would not be critical. Slider turtles display the typical reptilian activity pattern in response to seasons and temperatures. The periods of greatest overland and aquatic movement are in the spring and fall. During the winter, individuals become dormant, but in areas where winter observations have been made, some individuals are active on sunny days, even when water temperatures are below 4° C. Summer appears to be a period of reduced activity, relative to spring and fall. Some individuals estivate under banks or beneath terrestrial surface litter during periods of high temperature.

Although most slider turtles in the world die before they leave the nest, because of predation or other factors, those that reach the water and ultimately achieve adulthood have higher survival rates than most other animals. Sliders, as well as other species of turtles, live for more than a quarter of a century (Gibbons and Semlitsch, 1982; Gibbons, 1987). Senility does not seem to be a characteristic of slider turtles.

### Habitats and Relative Abundance of the Slider Turtle

A consideration of a species' population characteristics under different habitat conditions can establish whether the species is a habitat specialist or generalist and can provide insight into its ecology and evolutionary history. The slider turtle is unmistakably a habitat generalist, compared with other species of turtles. A survey of the habitats where slider turtles have been sampled by investigators conducting life history studies reveals the spectrum of habitats where sliders not only survive but also flourish. Slider turtles are noted for the ubiquity of their habitat throughout their range. Carr (1952) reported slider turtles from a wide variety of habitats, including intermittent streams, sloughs, sinkholes, and oxbow lakes. Cagle (1950), who conducted the most extensive natural history studies on the species in the United States, found populations living in lakes, ponds, swamps, slow-moving streams, and roadside ditches with little or no vegetation. Moll and Legler (1971) found tropical popula-

tions that inhabited large permanent rivers with abundant vegetation and contiguous backwaters. Legler (1960c) found Big Bend slider turtles (*T. s. gaigeae*) inhabiting large rivers in desert regions of northern Mexico.

Not surprisingly, then, slider turtles have been found in almost every conceivable aquatic habitat in, on, and around the SRP. These include Carolina bays that fluctuate from having water 2 m deep in some years to being dried-up fields in others; seepage basins with radioactive waste materials and a variety of chemical pollutants; farm ponds; natural stream systems; and the Savannah River. One population near the SRP is in a runoff habitat from a hog farm that is estimated to have more than 2,000 slider turtles occupying a body of water with an area of less than 2 ha. No other vertebrates live in the habitat, no aquatic invertebrates are apparent, and a sample of 6 turtles dissected by G. W. Esch at Wake Forest University had no helminth parasites. Thus, turtles are the only apparent, or at least one of the few, multicellular animals that can live in the habitat. Slider turtles can thrive even in waters receiving thermal effluent, as observed in an Illinois reservoir (Thornhill, 1982) and in the thermally elevated reservoirs, streams, and swamps of the SRP.

Primary limitations to the geographic range of slider turtles in the United States might at first appear to be cold weather along the northern edge of the range and arid conditions along the western edge, although the subspecies *T. s. nebulosa* apparently lives in situations in Baja California where drought is a constant specter (Carr, 1952), and the species clearly does well in Illinois, where winters can be harsh (Cagle, 1950). No ready explanation is available for why slider turtles occur in Florida's panhandle but not in the lower part of the state. Competition with *Pseudemys nelsoni* is suspected as an explanation, but no documentation is available to support this contention.

Turtles are an apparent and significant component of the vertebrate fauna of many freshwater, terrestrial, and marine systems, and numerous studies have focused on population features of various species. However, relatively little research with turtles has been directed toward interspecific interactions or other community and ecosystem considerations, although understanding the role of species components is considered to be of critical importance in such studies. This lack of research may be, in part, a consequence of turtles' usually being represented by only one or a few species in most habitats where they occur and of their constituting only a small proportion of the faunal biomass, individual numbers, and productivity. Nonetheless, their potential role in community function has been noted (Congdon and Gibbons, 1989a).

An important initial step toward understanding aquatic or terrestrial communities is to have accurate estimates of standing crop biomass and annual productivity of the species components. Initial steps have been taken toward understanding the role of turtles in aquatic ecosystems

(Congdon et al., 1986), but data on standing crop biomass are few and have usually been limited to single species (Iverson, 1982) rather than the whole turtle community. Estimates of biomass production in turtle species populations or communities are even rarer (Congdon and Gibbons, 1989a).

Many studies have reported estimates of population size and density for freshwater and terrestrial species; however, most density calculations have been based on rough estimates of population sizes and on arbitrary delineations of habitat boundaries. Few studies have considered species interaction among turtles (Berry, 1975), although studies on species composition and relative abundance, and their importance to competition and predation, have been presented for lizards (e.g., Dunham, 1980; Pianka, 1986).

We have compared standing crop and annual biomass productivity for several turtle populations in southern and northern freshwater wetlands (Congdon et al., 1986; Congdon and Gibbons, 1989a). Biomass production rates of turtles were estimated for a six-species community in a Carolina bay (Ellenton Bay) in South Carolina and for a three-species community in a marsh (East Marsh) in southeastern Michigan. *Trachemys scripta* was the numerically dominant species and had the highest standing crop biomass in most southern populations examined.

Of the six common species within the Ellenton Bay community, total biomass production (eggs plus soma) rates ranged from a low of 0.2 kg/ha/yr for *Sternotherus odoratus* to 5.2 kg/ha/yr for *T. scripta*. Total biomass production for the entire six-species community was 9.7 kg/ha/yr. In East Marsh, biomass production ranged from 1.8 kg/ha/yr for *Emydoidea blandingii* to 4.0 kg/ha/yr for *Chelydra serpentina*. Biomass production in the numerically dominant species, *Chrysemys picta*, was 2.4 kg/ha/yr. Total biomass production for the three-species community was 7.3 kg/ha/yr. This should not be taken as a definitive statement that southern turtle communities have a higher standing crop and biomass production rate than North Temperate ones, although this finding may serve as the basis for future comparisons.

Biomass production rates of turtles averaged less than 0.05% of the estimated total primary productivity of similar wetland habitats. Although the standing crop biomass and biomass productivity of turtles are dramatically lower than those of plants in aquatic systems, turtles have a potentially high impact on such systems, particularly in transient wetlands, and may have a previously unsuspected influence on natural wetland habitats that is disproportionate to their comparative standing crop biomass.

The few biomass estimates of single-species populations of turtles presented in the literature do not usually include all species in the habitat. However, enough information has been gathered that certain general hypotheses

can be advanced. Iverson (1982) gave a thorough review of the subject, concluding that (1) populations of herbivorous turtles tend to have higher biomasses than do either carnivorous or omnivorous species; (2) populations of semiaquatic species tend to have lower biomasses than do species that are primarily aquatic; and (3) islands, ponds, and springs, compared with all other habitats studied, have populations with the highest biomasses. In contrast, we (Congdon et al., 1986) have suggested that species-specific densities and biomass are more closely related to habitat suitability, body size of the species, and population age structure than to trophic position. Clearly, the topic is one deserving of further consideration.

The purpose of studying ecological patterns in the slider or any other turtle species is to be able to understand why turtles make decisions to do one thing rather than another. In the simplest measure and most basic terms, the goal of science is to have as firm a grasp as possible on natural phenomena, including the organisms with which we live. Knowing what the potential gains and expenses are to an individual turtle when it moves, eats, or breeds can give us not only a predictability about the behavior and activity patterns of turtles but also insight into the evolutionary background that has led to turtles' behaving the way they do. Knowing what turtles do may lead to ideas about other animals that may have faced similar decisions during their own evolution. The following sections consider fundamental steps in the life of slider turtles based on what is known today and may be instructive in posing questions for future studies.

### Life Movement Patterns of the Slider Turtle: An Overview

A premise in the discussion of movement patterns is that alternative choices relating to movement by individual turtles are ultimately under genetic control. It is not necessary to assume that a single allele is involved in any particular movement pattern, and in fact it is more likely that a variety of physiological and ecological considerations must be weighed in terms of their risks and benefits in a manner that natural selection can operate on. The changing probabilities of whether one movement pattern is more likely to be successful than another are an explanation for the inherent variability in movement patterns among individuals. However, consistent patterns of activity and movement in a population are identifiable in a generalized manner, which speaks to the shaping of movement strategies by natural selection through an inheritable genetic medium.

Based on the information available at this time, a scenario can be constructed using a risk-benefit analysis for why slider turtles move from one place to another during their lifetime. The initial travel by all species of freshwater turtles is from the nest to the water, and the decision by a



slider turtle about when to make the trip involves potential risks and benefits. Exposure to predators, desiccation, and thermal extremes, and the acquisition and apportionment of energy, are factors that can influence success or failure of the individual and are affected by the individual's choice of activity pattern.

Slider turtles from all reported areas characteristically delay emergence from the nest after hatching. In South Carolina even the clutches of eggs laid latest in the season complete incubation before the onset of cold temperatures. Therefore, the hatchlings are at a developmental state that would permit their departure from the nest cavity and entry into the aquatic environment in late summer or fall.

The benefits that could accrue to an individual from immediate departure from the nest upon hatching would be the initiation of growth at an earlier age and a subsequent size advantage. However, the risk of entering a habitat at an inopportune time can be high if resources are not available, because exposure to predators would be increased and growth would not be enhanced. In addition, it would be necessary in South Carolina to locate a sanctuary for the upcoming period of cold weather. The benefit of remaining in the nest is that the individual is already occupying a safe site prior to a several-month period that is likely to yield minimal returns energetically. A springtime emergence has the benefit of the highest assurance of available resources for a longer period of time.

One prediction regarding hatchling emergence is that in climatic regions where the end of the incubation period coincides with what will be a predictably long period suitable for growth, slider turtles should not delay emergence from the nest but enter the aquatic environment immediately. A corollary prediction is that in areas where the risk is increased for hatchlings that remain in the nest for an extended period, such as certain floodplain systems in which winter flooding is a common occurrence, natural selection should operate on any genetic component associated with the timing of emergence, and immediate emergence from the nest should be the rule. Because it is unknown how labile the timing of emergence might be genetically, it is uncertain whether immediate or delayed departure from the nest might be habitat-specific, with some populations of sliders or other species exhibiting one approach and other populations in that same region exhibiting another. This is an interesting problem that bears investigation.

Once a slider turtle has entered the aquatic environment, movement as a juvenile should be limited to the location of effective areas for eating, basking, and inactivity at night and during cold weather. In situations where habitat conditions remain stable, I see no reason why juvenile slider turtles should travel other than intrapopulationally, and even then only to the extent of taking

advantage of microhabitat distributions of resources. Small turtles characteristically limit their activity to areas of heavy floating vegetation and would incur the risk of exposure to predators by making any excursions outside such areas, especially trips across open water.

Preliminary evidence indicates that juvenile turtles become active later in the spring and retire earlier in the fall than adults, presumably because the benefit of limited food acquisition does not outweigh the increased exposure to predators. One possible explanation for extensive intrapopulation or even extrapopulation movement by juvenile turtles is exploratory behavior that might benefit the individual by giving it a more complete awareness of the resource potential of the local habitat and surrounding areas. A prediction is that wanderlust in juvenile turtles inhabiting an area of adequate resources increases as a function of body size, which would reduce the risk of susceptibility to predators.

In slider turtle habitats with adequate resources, extrapopulation movement associated with reproduction should not commence until an individual reaches maturity. The potential benefits to a male slider turtle for moving from one body of water to another are an increase in encounters with females and the subsequent increase in fitness if mating can be achieved. The potential risks are not only exposure to a new suite of predators but also the possibility of being in the terrestrial environment during unexpected environmental extremes, such as a cold front or a prolonged period of high temperatures. Any of these risks would presumably diminish with an increase in size of the animal. Indeed, long-distance travel is proportionately higher in larger individuals than smaller ones. One aspect of overland travel between bodies of water that deserves mention is the question of how slider turtles initially make such a move. Although documentation has not been presented at this time, I hypothesize that slider turtles, and perhaps other species that are frequent interhabitat transients, are able to detect the presence of other bodies of water visually by some mechanism involving the properties of reflected light. Sun-compass orientation has been demonstrated in the closely related *Chrysemys picta* (DeRosa and Taylor, 1982), but this would be of little value unless the individual has visited another site on a previous occasion. Although long-distance movements should be abruptly correlated with the attainment of maturity and the clear benefits to be derived from overland travel, intrapopulation movements should increase throughout the population with an increase in body size that would result in more effective utilization of microhabitat resources with increased impunity from predation.

The primary terrestrial movements of female freshwater turtles are associated with nesting activities. A size-related aspect of nesting excursions might be that larger females would be at less risk during terrestrial excursions than would smaller females. A benefit could definitely be

derived from extensive searching by the female until she locates a site she considers highly suitable for nesting. I am unaware of any study that has considered the relationship between body size of females and the amount of distance covered and times spent on land in search of nesting sites, although nesting studies conducted on the George Reserve in Michigan could address this question (Congdon, pers. com.). If large females are more likely than small females to make long nesting forays, large females would be more likely to approach the vicinity of aquatic habitats other than the one in which they normally reside. Thus, larger females would be expected to relocate at greater distances from their original aquatic habitat.

The final area of concern regarding movement patterns is that of travel that is not a predictable seasonal or age-related response but is a response to conditions that are unsuitable for the individual. In this situation the potential benefits of overland or aquatic travel have a greater than even probability of outweighing the risks of such travel. Travel that finds its basis in conditions that are unsuitable for an entire population is of course more likely to be observed, because individuals of all or many size and age classes respond. Even as juveniles, individuals are confronted with situations in which resources may be less than desirable, so a decision must be made as to whether travel is warranted in terms of the risks that might be encountered in the search for more suitable habitat.

A testable hypothesis that seems reasonable is that individuals would respond differently to a particular resource situation and would evaluate the risk-benefit ratio differently, which would of course explain the variability observed among individuals in their propensity to engage in overland travel. Resources for juveniles would presumably be restricted to those involving opportunities for growth and survival, whereas those for adults would have the added component of reproductive success. Larger body size would presumably confer an advantage in reducing predator and environmental risks to turtles; therefore, the documentation of a correlation between movement, particularly overland travel, and body size would be expected for other species as well. Even small turtles are observed in transit between bodies of water, possibly because the potential benefits of available resources have diminished to a level that the risk of movement is judged to be less than the potential benefits to be derived elsewhere.

### **Lifetime Energetics Decisions of the Slider Turtle**

As with movement, the initial decision point in the life cycle of a turtle regarding energy apportionment and acquisition comes while the turtle is in the nest. Energy will be expended whether the turtle remains in the nest or attempts to enter the aquatic environment, but only the latter approach offers any opportunity to acquire addi-

tional energy through feeding. It is possible, however, for the turtle to enter the aquatic environment at an inopportune time for foraging such that lipid stores of the embryo may be used during a futile effort to find food. This then becomes an additional factor associated with the decision not to leave the nest at what may seem to be a propitious time in the fall.

The energy required by a juvenile can be partitioned primarily into that required for maintenance and that required for growth. Presumably, a juvenile turtle will eat and grow at the maximum rate that is possible under the circumstances. The variability observed among individuals within a population presumably reflects the variability in opportunities each has had in foraging in different microhabitats. I can see no reason why juvenile turtles, prior to the advent of any secondary sexual traits or other changes associated with incipient maturity, should differ in their growth rates and patterns of growth on the basis of sex. Achieving a large size as rapidly as possible should be of equal benefit to either sex and thus be equally favored by natural selection. I know of no evidence to the contrary in turtles, and our evidence from slider turtles in South Carolina is that males and females grow at equal rates when they are immature. However, because male slider turtles begin to reach maturity at a smaller size than females, their growth rate slows considerably relative to that of immature females that are the same size. It is at this point in a slider turtle's life history that males begin to partition energy resources into reproduction in lieu of growth.

The mortality risks and energetics costs associated with reproductive activity in male turtles are probably less well appreciated than are those for female turtles, in which egg production and nesting are so obvious. However, a male's reproductive fitness can be equated with the number of successful mating encounters. The probability of successful mating would presumably increase in relation to the probability of finding receptive females (Fig. 1.2). A male turtle in search of females, especially when the search entails long-distance excursions, experiences major metabolic costs for its activity and spends less time foraging and acquiring energy resources. Although it has not been documented, my assumption is that males divert all available energy into such reproductive activity until all possibilities of locating receptive females have been exhausted.

The apportioning of energy by female slider turtles is possibly easier to measure because of the relative ease by which egg production can be expressed quantitatively in terms of energy. However, measurements have not been made of the energetics expenditures for various forms of reproductive activity, such as searching for proper nesting sites, so-called prenesting exploratory behavior, and the documented overland and aquatic movement of immature females that are large but not reproductively active. Nor is the cycle of energy transfer from lipid stores into

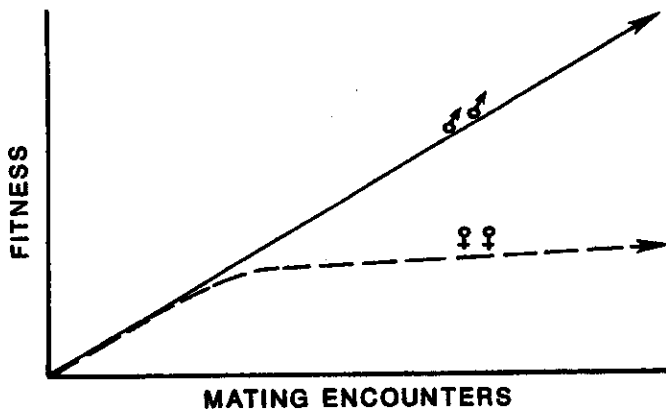


FIGURE 1.2. Relationship between potential reproductive fitness and number of mating encounters of both sexes of the slider turtle, a species whose females are capable of sperm storage.

ovarian follicles fully understood (Tinkle et al., 1981).

In the final years of life, both mature males and mature females would presumably partition their energy resources in a manner that emphasizes reproduction at the cost of growth. However, the observation of continued growth in large individuals in both sexes suggests that in certain years there may be circumstances in which the reproductive effort is expended for the year, and the acquisition of resources can be converted into an increase in body size. I imagine that careful measurements of the seasonal timing of growth in adult turtles would reveal that the major portion of incremental growth occurs after any potential for reproductive activity between the sexes has ceased. Also, because available lipid reserves would presumably have been shunted into reproduction, and the initial energy harvested would be used for replenishing those reserves, a lag time between the end of reproductive activity and the initiation of any growth in body size of adults would be expected.

Clearly, these are matters for future investigations and will be resolved through the gathering of careful empirical evidence both in natural situations and experimentally. The life history questions associated with bioenergetics are some of the most intriguing ones turtle biologists will face during the next few years.

### Literature Survey

One problem that certainly will become more prevalent with the increase in scientific knowledge is the unintentional omission of pertinent references through oversight or ignorance. I assume that the intentional omission of references because someone does not like someone else will stay at about the same level as always. Not citing a publication because of personal animosities or insecurities is of course petty and unprofessional, as I am sure all who are professional and not petty would agree.

I have no delusions of any sort that every reference of turtle biology that would be appropriate in this book has been cited. I speak not only for myself but also for any of the other authors when I apologize for the omission of studies that should have been included somewhere but were not. Furthermore, I request that the author of the chapter be notified of such errors so that the appropriate citation can be given if subsequent editions of the book are printed. Scientists are often reluctant to make a case that their own work should have been cited in a particular presentation. In many instances, however, an uncited author would be providing a service by making another author aware of such omissions.

One source of literature that can sometimes be overlooked because of its unavailability is doctoral dissertations and master's theses. A list of the doctoral dissertations from the United States that have been written about turtles and of which I am aware are listed in Appendix 1.2. I have not attempted to list the numerous master's theses that have focused on the biology of turtles, although many outstanding ones are shelved away in biology departments around the country. Turtle biologists will recognize many of the dissertations because of the open-literature publications that resulted from them. However, a great deal of useful information about turtles is still harbored in dissertations and theses that will never be published.

### Acknowledgments

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APPENDIX 1.2. Doctoral dissertations pertinent to studies on the life history, ecology, or evolution of turtles

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- Ackerman, R. A.  
1975. Diffusion and the gas exchange of sea turtle eggs. University of Florida.
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1966. Leptospiral flora of aquatic turtles in Illinois. University of Illinois.
- Barone, M. C.  
1968. Effect of induced cold torpor and time of year on blood coagulation, serum proteins, and other blood properties of the turtles *Pseudemys scripta* and *Chrysemys picta*. St. Bonaventure University.
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1980. Orientation and homing of the wood turtle (*Clemmys insculpta*). Rutgers.
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1966. A study of brain and cervical spinal cord in *Chrysemys picta*. St. Louis University.
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1970. An investigation on the effect of cold exposure on the cardiac metabolism of the turtle, *Chrysemys picta*. State University of New York at Buffalo.
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1961. Anaerobic mechanisms in the diving of the loggerhead musk turtle, *Sternotherus minor*. University of Florida.
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1974. Studies on the population dynamics of helminth parasites in the yellow-bellied turtle, *Pseudemys scripta scripta*. Wake Forest University.
- Boyer, D. R.  
1958. Biological implications of the basking habit in turtles. Tulane University.
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1971. Comparative blood studies of turtles as related to environment and tolerance of submersion. University of Southern Mississippi.
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1977. Evolution in karyotypes: I. Sex determination, and II. Chromosomes of side-necked turtles. University of Utah.
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1972. Habits and home range of the pacific pond turtle, *Clemmys marmorata*, in a stream community. University of California, Berkeley.
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1973. A qualitative and quantitative electron-microscopic study of the retina of the turtle, *Pseudemys scripta elegans*. University of Delaware.

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1943. The growth of the slider turtle, *Pseudemys scripta elegans*. University of Michigan.
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1983. Passive electrical properties of horizontal cells in the retina of the turtle, *Pseudemys scripta elegans*. University of Illinois.
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1983. The renin-angiotensin system in the freshwater turtle *Pseudemys scripta*. University of Illinois.
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1971. Studies on anaerobic metabolism in the freshwater turtle (*Pseudemys* species). University of North Carolina at Chapel Hill.
- Cowan, F. B. M.  
1970. Comparative studies on the cranial glands of turtles with special reference to salt secretion. University of Toronto.
- Crenshaw, J. W., Jr.  
1955. The ecological geography of the *Pseudemys floridana* complex in the southeastern United States. University of Florida.
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1985. The biology and conservation of sea turtles in North Carolina (marine, population, *Caretta caretta*, demography, Georgia). University of Wisconsin—Madison.
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1920. Some phases in the development of *Chrysemys cinerea*. University of Wisconsin—Madison.
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1975. Variation in the cranial feeding mechanism of turtles of the genus *Trionyx geoffroy*. University of Toronto.
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1964. The role of the kidneys and bladder in the handling of water and solutes in the freshwater turtle, *Pseudemys scripta*, and the desert tortoise, *Gopherus agassizii*. Duke University.
- Davis, M.  
1981. Aspects of the social and spatial experience of eastern box turtles, *Terrapene carolina carolina*. University of Tennessee at Knoxville.
- DeRosa, C. T.  
1977. A comparison of orientation mechanisms in aquatic, semi-aquatic, and terrestrial turtles (*Trionyx spinifer*, *Chrysemys picta*, and *Terrapene c. carolina*). Miami University.
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1984. The organization of the cerebral cortex of the pond turtle, *Pseudemys scripta elegans*. Harvard University.
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1966. Reproduction and growth in the alligator snapping turtle, *Macrolemys temmincki* (Troost). Tulane University.
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1969. Natural history and ecology of the painted turtle, *Chrysemys picta* (Schneider). University of Kentucky.
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1966. Variation in snapping turtles, *Chelydra serpentina* Linnaeus: A study in quantitative systematics. University of Utah.
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1973. Aerobic and anaerobic metabolism during activity in the turtles *Pseudemys scripta* and *Terrapene ornata*. University of Michigan.
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1967. Population dynamics and ecology of the painted turtle, *Chrysemys picta*. Michigan State University.
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1984. Life history energetics of the red-eared turtle, *Pseudemys scripta*, in north central Texas (reptiles). North Texas State University.
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1972. Temperature-photoperiod effects on diel locomotor activity and thermal selection in the turtles *Chrysemys picta* (Schneider), *Clemmys guttata* (Schneider), and *Sternotherus odoratus* (Latreille). University of Rhode Island.
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1984. The chemosensory behavior of juvenile sea turtles: Im-

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1984. The influence of environmental factors on eggs and hatchlings of painted turtles (*Chrysemys picta*). Colorado State University.
- Hammer, D. A.  
1973. Ecological relations of waterfowl and snapping turtle populations. Utah State University.
- Hart, D. R.  
1979. Resource partitioning among Louisiana turtles of the genus *Chrysemys*. Tulane University.
- Hartweg, N. E.  
1934. A study of genetic variation in the genus *Chrysemys*. University of Michigan.
- Hartwell, E. M.  
1881. Notes on some points in the anatomy and physiology of the slider terrapin (*Pseudemys rugosa*). Johns Hopkins University.
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1983. The physiological responses of the turtle, *Chrysemys picta bellii*, to apnea, as a function of temperature. Brown University.
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1964. The effect of bleeding and starvation on erythropoiesis in the turtle, *Pseudemys scripta elegans*. New York University.
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1984. Studies on the immunoparasitology of eastern painted turtles (*Chrysemys picta picta*) and snapping turtles (*Chelydra serpentina*) exposed to spirorchid blood flukes (*Spirorchis scripta*). University of Rhode Island.
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1977. The fossil freshwater emydid turtles of Florida. University of Florida.
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1976. Comparative osteology of *Graptemys flavimaculata* Cagle and *Graptemys nigrinoda* Cagle (Testudines, Emydidae). University of Arkansas.
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1940. Ecological studies of turtles in Michigan with special reference to fish management. University of Michigan.
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1959. The life history and ecology of the ornate box turtle, *Terrapene ornata ornata* Agassiz. University of Kansas.
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1953. Biophysical and biochemical studies of the blood of the central painted turtle: *Chrysemys picta marginata*. St. Louis University.
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1975. Cardiovascular and respiratory responses to temperature, diving, carotid occlusion and hemorrhage in the turtle *Pseudemys scripta elegans*. Idaho State University.
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