

Esch, Gerald W., David J. Marcogliese, Timothy M. Goater and Kym C. Jacobson. 1990. Chapter 23. Aspects of the Evolution and Ecology of Helminth Parasites in Turtles: A Review. pp. 299-307. In *Life History and Ecology of the Slider Turtle*, J. Whitfield Gibbons (ed.). Smithsonian Institution Press. Washington, D.C.

23

GERALD W. ESCH
DAVID J. MARCOGLIESE
TIMOTHY M. GOATER
KYM C. JACOBSON
Department of Biology
Wake Forest University
Winston-Salem, North Carolina 27109

Aspects of the Evolution and Ecology of Helminth Parasites in Turtles: A Review

Abstract

This chapter presents a review of the evolution and ecology of the helminth parasites of turtles, with primary emphasis on the slider (*Trachemys scripta*). Turtle parasites have probably undergone little adaptive radiation since turtles appeared in the Triassic. Species of nematodes and trematodes are well represented in turtles, but cestodes and acanthocephalans are not. Several studies have shown that seasonality, habitat stability, and ontogenetic shifts in diet are significant factors in influencing parasite populations in *T. scripta*. A comparative approach reveals that turtle feeding patterns are critical in affecting species diversity of helminth communities. The question of whether competition is an important structuring mechanism in the parasite communities in turtles is addressed. Recent results indicate that competitive interactions are minimal among four acanthocephalan congeners of *T. scripta*, because the four are both linearly and circumferentially sympatric in the host intestine. Future research should be directed at parasite intrapopulation dynamics and parasite biogeography in relation to turtle dispersal patterns. Such an approach would be valuable in addressing rapidly emerging concepts of parasite ecology as well as providing a useful source of information regarding the evolution and ecology of turtles.

Introduction

Parasitism, broadly defined, is a symbiotic relationship whereby one member of the association (the parasite) lives at the expense of the other (the host). More than 50% of the world's described organisms are parasitic in nature, and virtually every plant and animal species is, to some extent, parasitized during its life history (Price, 1980). Clearly, the success of the parasitic lifestyle is remarkable. Yet, surprisingly, only relatively recently have ecological

and evolutionary concepts emerged for this diverse and highly successful group of organisms.

This review deals with the evolution and ecology of helminth parasites (Trematoda, Cestoda, Acanthocephala, and Nematoda) of turtles, with special emphasis on those of the slider turtle (*Trachemys scripta*). Investigators typically overlook the potential of using helminths as biological indicators of ecological relationships between hosts in terms of trophic interactions, migratory movements, foraging behaviors, and phylogenetic relationships. Many helminths have complex life cycles and, thus, commonly exploit food-web interactions, particularly predator-prey relationships, to effect transmission. Furthermore, because parasites have coevolved with their hosts, they are potential tools for understanding the evolutionary history of host species. These attributes present unique and valuable opportunities for developing additional insights into the ecology and evolution of the hosts that they infect.

We divide our review on the helminth parasites of turtles into two broad categories. The first emphasizes the systematics, taxonomy, and phylogenetic relationships between helminth parasites and their chelonian hosts. It focuses on reviewing the types of helminths infecting turtles, offering explanations for why some helminth taxa are depauperate, although others are well represented.

The second section of the review is concerned with the potential use of helminth parasites as indicators of turtle biology. First, we review the major theoretical concepts in parasite ecology, providing a framework for the remaining discussion. Second, we review certain critical features of slider turtle ecology and how factors such as host diet, age, temporal and spatial parameters, and seasonality influence the slider's parasite population dynamics. Third, helminth species diversities in a variety of turtles spanning aquatic to terrestrial habitats are examined within the context of several recent ecological concepts developed by Holmes and Price (1986) and Kennedy et al. (1986). Fourth, we examine what is probably the most contentious topic in community ecology, that is, the extent to which biotic interactions are important in structuring communities. In addressing this question, we illustrate the powerful comparative approach used in investigating patterns of helminth co-occurrence and structure within enteric helminth communities.

Finally, we conclude with prospects for future research employing turtles and their helminth parasites as study systems. We hope that the approach used in this review will entice further investigators to recognize the potential for using helminth parasites to assess evolutionary and ecological questions relating to their vertebrate hosts.

Evolutionary Considerations

The range of helminth parasite taxa infecting turtles is wide, extending from the primitive aspidogastrea trem-

atodes to the highly specialized acanthocephalans. Previously, it was believed that helminths evolved more slowly than their hosts. More recently, however, Price (1980) reasoned that certain properties of parasite populations, such as short generation times, large populations relative to the host, and isolated subpopulations of parasites, have led to high evolutionary capabilities. Therefore, parasites have been able to track evolutionary changes in their hosts and adapt to changing conditions quickly. Brooks (1979) suggested that the evolutionary history of a parasite taxon reflects the evolutionary history of the host. For example, he proposed that the digenean trematodes of crocodylians have coevolved with their hosts. Furthermore, the radiation of species of *Glyphelmis* (Trematoda) and pro-teocephalid cestodes has paralleled that of some anuran and salamander families (Brooks, 1977, 1978). Indeed, if the evolutionary history of a host is indicated by its parasite fauna, stability in a host lineage after a burst of adaptive radiation should be reflected by the parasites of that host (Baker, 1984). Chelonians appeared on the evolutionary scene early in the Triassic, 225 million years ago. These Mesozoic taxa differ little from their present-day counterparts (Martof et al., 1980). As a consequence, turtle parasites have undergone little adaptive radiation since the appearance of turtles in geologic history, certainly less radiation than parasites within the other major vertebrate taxa.

If one examines the geographic distribution of 21 families of nematodes that presumably evolved in reptiles and amphibians (Baker, 1984), 9 of 12 families found in turtles are cosmopolitan, and 1 other is found in at least six of the world's seven geographic regions (as defined by Baker, 1984; Table 23.1). If a cosmopolitan distribution indicates an older evolutionary age in a group, then it is suggested that there has been little opportunity for geographic isolation and subsequent adaptive radiation among turtle parasites.

On the other hand, certain components of the turtle parasite fauna do not reflect the evolutionary history of the host. That is, certain parasites have been acquired

Table 23.1. Geographic regions inhabited by families of nematodes that presumably evolved in amphibians and reptiles and in chelonians

Number of regions	Number of families	
	Amphibians and reptiles	Chelonians
0	—	9
1	1	0
2	2	1
3	3	1
4	1	0
5	0	0
6	1	1
7 (= cosmopolitan)	13	9

Note: Regions are from Baker (1984).

from other vertebrates by the so-called host-capture phenomenon, a common occurrence in the evolutionary history of the nematodes of vertebrates (Chabaud, 1981). However, Holmes and Price (1980) cautioned that these captured species, because of their subsequent speciation, will be difficult to distinguish from parasites that have had a long evolutionary association with their hosts. They noted that there are many generalist parasites with excellent potential for colonization and that these parasites will reflect the ecological, not the phylogenetic, history of the host. Baker (1984) asserted that captured parasites can be distinguished from heirloom parasites (whose ancestors were harbored by the host's ancestors) when the latter groups have a narrow host range and thus can be assumed to have evolved with their hosts. In contrast, captured parasites have a higher proportion of related genera and species in nonrelated host taxa.

An excellent review of the capture phenomenon is provided by Baker (1984) for nematodes parasitic in amphibians and reptiles. There are approximately 1,040 nematode species in amphibian and reptilian hosts. Of these, 146, or approximately 14%, are primarily parasites of chelonians. A relatively small number of nematode taxa (8 genera consisting of 22 species) are presumed to have originally evolved in invertebrates, fish, birds, or mammals (Table 23.2). As Baker et al. (1987) stated, "The presence of isolated monobasic genera in hosts such as salamanders and freshwater turtles represents individual parasite captures by these hosts in an aquatic habitat." These genera represent species from widely separated and geographically isolated localities, as well as those with a variety of life cycle patterns. Baker (1984) suggested that either they have been only recently acquired or they represent relatively long associations that have been unsuccessful in evolving further among their acquired host groups, presumably because of the stability of chelonian evolutionary history. With only 22 of 146 nematode species having been captured, the majority evolved directly with their hosts and represent long-term, coevolutionary partners. The latter group includes species of oxyuridans, ascarididans, spiruridans, and strongylidans. Most of the nematode families possess a widespread distribution with little opportunity for speciation beyond the initial adaptive radiation that occurred during the Triassic. The great reptilian adaptive radiation at that time allowed for parallel radiation among reptilian parasites, with little phylogenetic splitting having occurred since.

It is feasible that other parasitic helminth taxa may have been captured as well. Digenetic trematodes show a high degree of specificity for their molluscan intermediate hosts. This indicates a long-standing evolutionary relationship between the Mollusca and Digenea and suggests the trematodes were primarily parasites of mollusks, with other intermediate and definitive hosts having been acquired during their subsequent evolutionary history.

Table 23.2. Nematode parasites of chelonians that presumably evolved in invertebrates, fish, birds, or mammals

Parasite	Number of genera in turtles	Number of species in turtles	Total number of genera
Ascaridia			
Seuratoidea			
Cucullanidae			
Cucullaninae	2	5	4
Ascaridoidea			
Anisakidae			
Anisakinae	1	1	6
Spirurida			
Camallanoidea			
Camallanidae			
Camallaninae	2	13	5
Dracunculoidea			
Dracunculidae	1	1	2
Physalopteroidea			
Physalopteridae			
Proleptinae	1	1	4
Filarioidea			
Onchocercidae			
Splendidofiliariinae	1	1	16

Source: Condensed from Baker, 1984.

Thus, they have been amenable to capture by other taxa, including turtles. Cestodes, on the other hand, are suspected of having evolved initially in vertebrates, leading to increased host specificity for their definitive hosts. Generally, acanthocephalans are relatively host-specific, which implies a long coevolutionary history between them and their definitive hosts.

Turtles span a range of aquatic to terrestrial habitats and vary widely in their life histories and ecology. We believe that the relative paucity of acanthocephalan and cestode species in turtles is not related to habitat, behavior, or dietary preferences of the turtle hosts. The basis for this assertion rests with the knowledge that other vertebrate taxa are, generally, richly endowed with a wide mix of these helminth taxa, with chelonians being the exception (see Table 23.3). A taxonomic synopsis of chelonian parasites lends partial support to this notion. Approximately 70 families and 400 genera of digenetic trematodes infect vertebrates (Schell, 1980). Of this number, at least 21 families and 72 genera of trematodes are associated with chelonians; 11 families and 37 genera of nematodes are associated with chelonians (Ernst and Ernst, 1977). Yamaguti (1963) lists 37 families and 108 genera of acanthocephalans in vertebrates. Among turtles, however, there are only 1 family, 2 genera, and 8 species of acanthocephalans. Of the 58 families of Cestoda infecting vertebrates, only 1 is known to infect turtles (Ernst and Ernst, 1977).

A phylogenetic approach, based on the assumption that parasites characterize a host in much the same way as its morphological, cytological, and biochemical traits do, was used to examine the nature of phylogenetic relation-

Table 23.3. Checklist of the helminth parasites of *Trachemys scripta*

Trematoda	
Monogenea	
1. <i>Neopolyostoma domatiliae</i> ^a	
2. <i>N. orbiculare</i>	
3. <i>Polystomoidella hassalli</i>	
4. <i>P. oblongum</i>	
5. <i>Polystomoides coronatum</i>	
Digenea	
1. <i>Allassostoma magnum</i>	
2. <i>Cephalogonimus vesicaudus</i>	
3. <i>Diclyangium chelydrae</i>	
4. <i>Heronimus chelydrae</i> ^a	
5. <i>H. mollis</i>	
6. <i>Macrovestibulum kepneri</i>	
7. <i>M. obtusicaudum</i>	
8. <i>Pneumatophilus variabilis</i>	
9. <i>Protenes angustus</i>	
10. <i>Schizamphistomoides tabascensis</i> ^a	
11. <i>Spirochis artericola</i>	
12. <i>S. blandingioides</i>	
13. <i>S. elegans</i>	
14. <i>S. pseudemydae</i>	
15. <i>S. scripta</i>	
16. <i>Telorchis cori</i>	
17. <i>T. diminutus</i> ^a	
18. <i>T. medius</i> ^a	
19. <i>T. nematoides</i>	
20. <i>T. robustus</i>	
21. <i>T. singularis</i>	
22. <i>Unicaecum dissimile</i>	
23. <i>U. ruzskowskii</i>	
Cestoda	
1. <i>Proteocephalus testudo</i>	
Acanthocephala	
1. <i>Leptorhynchoides</i> sp.	
2. <i>Neoechinorhynchus chelonos</i>	
3. <i>N. chrysemidis</i>	
4. <i>N. constrictus</i> ^a	
5. <i>N. emydis</i>	
6. <i>N. emyduoides</i>	
7. <i>N. magnapapillanus</i>	
8. <i>N. pseudemydis</i>	
9. <i>N. stunkardi</i> ^a	
Nematoda	
1. <i>Aplectiana</i> sp.	
2. <i>Camallanus microcephallus</i>	
3. <i>C. trispinosus</i> ^a	
4. <i>Chelonidracunculus</i> sp.	
5. <i>Cissophyllus penius</i>	
6. <i>Cucullanus cirratus</i>	
7. <i>Gnathostoma procyonum</i>	
8. <i>Icosiella quadrituberculata</i>	
9. <i>Oxyuroides</i> sp.	
10. <i>Spironoura</i> sp.	
11. <i>S. affinis</i>	
12. <i>S. chelydrae</i>	
13. <i>S. concinnae</i>	
14. <i>S. gracilis</i>	
15. <i>S. procera</i>	
16. <i>Spiraxys constrictus</i>	
17. <i>S. cordatus</i>	

Source: Ernst and Ernst, 1977.

^aThese parasites have been added to the checklist since Ernst and Ernst (1977).

ships among three emydid turtle genera—*Chrysemys*, *Pseudemys* (= *Trachemys*), and *Graptemys* (Ernst and Ernst, 1980). As outlined above, the degree of parasite host specificity can be used to demonstrate kinship of related species and is, therefore, appropriate for establishing phylogenetic affinities between hosts. After compiling a complete parasite checklist for host species within the three genera, Ernst and Ernst (1980) used the Index of Similarity developed by Sorensen (1948) for expressing generic relationships of the helminth faunas of the turtles. They concluded that similarity indexes of the helminth faunas in North American species of *Chrysemys*, *Pseudemys* (= *Trachemys*), and *Graptemys* show these to be separate turtle genera. They also indicated that species of *Trachemys* are not congeneric with *Chrysemys picta*, as has been previously suggested by other investigators (Zug, 1966; Weaver and Rose, 1967). Ernst and Ernst (1980) further concluded that species of *Graptemys* seem to be more closely allied taxonomically to *Trachemys* than to *Chrysemys picta*. Recently, Seidel and Smith (1986) recognized *Chrysemys* and *Trachemys* as distinct genera, based on morphological, biochemical, and paleontological evidence.

Although Brooks (1981) criticized some of the conclusions of Ernst and Ernst (1980), he recognized the value of comparing parasite faunas to solve problems of phylogenetic relationships between hosts. A more rigorous

analysis of the phylogenetic relationships of all parasite taxa in chelonians, coupled with further investigations of captured versus heirloom parasites, will be extremely productive in elucidating turtle evolutionary histories.

Ecological Considerations

Dogiel (1962) indicated that ecological parasitology is concerned with the study of the relationship between a parasite fauna treated as a unit on the one hand, and the changes in the environmental and physiological conditions of the host on the other. This description recognizes an essential feature of parasitism in that it emphasizes a relationship between two species populations. It remained for Crofton (1971) to delineate the elements of this relationship clearly and, moreover, to formulate a quantitative approach to understanding these elements. Crofton indicated that parasites are physiologically dependent on their hosts, are capable of killing heavily infected hosts, and have a higher reproductive potential than their hosts and that transmission dynamics of the parasite produce a contagious frequency distribution within the host population. In effect, a few hosts will carry most of the parasites and, thereby, limit potential negative effects to a few individuals within the host population.

At the population level, the quantitative concepts of Crofton (1971) were refined by Esch et al. (1975). They recognized that there are fundamental differences between the population dynamics of free-living organisms and helminth parasites. They defined a population as a group of organisms of the same species occupying a given space, but they stated that such a definition was inappropriate for most helminth parasites. The dilemma is clear when one asks whether parasites of a given species within a single host constitute a population or whether all members of a given parasite species within an ecosystem should be considered a population. They went on to point out that a population of free-living organisms increases in number through birth and/or immigration, whereas the number of helminth parasites within an individual host can usually increase only through immigration (recruitment). To provide an orderly means of assessing the dynamics of parasite population biology, Esch et al. introduced the concepts of the infrapopulation and the suprapopulation. They defined the former as all of the parasites of the same species within a given host. A suprapopulation was defined to include all the members of a given parasite species, in all stages of development, within an ecosystem. More recently, Riggs et al. (1987) introduced another term, "metapopulation," to describe all of the infrapopulations sampled from a given host species within an ecosystem. Given the complexity of parasite life cycles and the intricacy of host-parasite interactions, the concepts just outlined provide a systematic approach for the study of parasite populations at all levels.

In general, ecological theory as applied to communities has been developed through studies on free-living animals, with little attention given to specialist organisms such as parasites. P. Price (1980, 1984) accurately emphasized that specialists, such as parasites, are fundamentally different from more generalized free-living organisms and that, as a consequence, the organization of specialist communities may be fundamentally different from that of generalist communities.

Despite these apparent differences between specialist and generalist communities, Holmes and Price (1986) argued that helminth parasite communities have certain attributes that should permit them to contribute to several basic concepts in community ecology. First, helminth communities have discrete and unambiguous boundaries; that is, they occur within a host. Second, individual helminth communities from different hosts can be treated as replicates. Therefore, studies of comparative parasite community structure are powerful, because the host can be replicated through time and space much more readily than habitats for free-living organisms. Hosts with equivalent morphological structures (i.e., intestine, kidney, lung, etc.) are capable of supporting similar parasite communities in terms of parasite diversity and abundance. When they do not harbor similar parasite faunas, then the ecological and evolutionary mechanisms creating deficiencies in some hosts and not in others can be inferred. Third, an important factor known to influence the structure and dynamics of many free-living communities is predation. In parasite communities, predation does not occur, which means that this variable need not be considered in the analysis of parasite community structure and dynamics.

Holmes and Price (1986) developed a set of theoretical considerations suggesting that helminth infracommunities (parasite assemblages within individual hosts) span a continuum ranging from isolationist to interactive. Isolationist communities arise when the colonization abilities of parasites within the infracommunities are limited in scope. In isolationist infracommunities, biotic interactions such as competition are limited, and species diversity is low. On the other hand, interactive infracommunities occur when the colonization abilities of the parasites are high. Generally, interactive infracommunities have greater species diversity and tend to have higher parasite densities than isolationist infracommunities do. Within interactive infracommunities, there is more opportunity for biotic interaction, such as competition.

Holmes and Price (1986) recognized two other levels of hierarchical community organization among parasitic helminths (also see Root, 1973, who originally developed and discussed these concepts). The first is the component community, which includes all of the parasite infracommunities within a host species population. The second is the compound community, which consists of all of the

helminth infracommunities within a community of host species.

Throughout the world, turtles comprise a large component of the vertebrate fauna of many freshwater habitats (Congdon et al., 1986), yet few investigators have studied the parasites of these long-lived vertebrates from the standpoint of their ecology. However, there is enough information available to make certain generalizations and predictions regarding the factors influencing turtle parasite populations and communities.

HOST AGE AND DIET

Many helminths colonize turtles through accidental ingestion or active predation of intermediate hosts. Consequently, helminth parasites reveal certain features of turtle ecology. Age and diet are inextricably linked in the recruitment of helminth parasites by turtles. The basis for this generalization rests with the knowledge that in many turtle species, juveniles are obligate carnivores, but adults are primarily herbivorous (Marchand, in Carr, 1952; Clark and Gibbons, 1969).

The relationship between age and diet in turtles is confirmed by an analysis of parasite recruitment patterns in two closely related species, *Trachemys scripta* and *Chrysemys picta*. Esch and Gibbons (1967) reported a relationship between nematode densities and host age in a population of *C. picta* in hypereutrophic Wintergreen Lake in southwestern lower Michigan. Mean densities of the nematodes increased through the turtles' first 4 years and then declined as the turtles aged beyond 5 years. This pattern also held for trematodes in the same host population. All species of nematodes and trematodes in the Wintergreen Lake fauna are transmitted via invertebrate intermediate hosts, mostly arthropods, which indicates a change in host diet as the turtles age beyond 4 years.

Except for two species of trematodes in *T. scripta* collected from a variety of habitats on the Savannah River Plant (SRP) in South Carolina, significant correlations were observed between densities of enteric helminths and host plastron length, weight, and length of intestine (Esch et al., 1979a). However, parasite densities tended to increase in *T. scripta* beyond 4 years of age. This observation was especially pronounced for infrapopulations of acanthocephalans (*Neoechinorhynchus* spp.). The explanation offered by Esch et al. (1979a) was that as *T. scripta* become older and larger, their diet consists of greater quantities of aquatic vegetation. The intermediate hosts for *Neoechinorhynchus* spp. are several species of ostracods, which are important components of the epifauna associated with the vegetation on which the turtles feed. It should be emphasized that the increase in densities of *Neoechinorhynchus* spp. is not a consequence of parasite accumulation over time, because these helminths are short-lived, being turned over and recruited on an annual basis.

SEASON

Seasonal changes in parasite infrapopulation densities in turtles are known to occur, but they also appear to be influenced by latitude. Esch and Gibbons (1967) reported that densities of nematodes in the Wintergreen Lake *C. picta* population appeared to increase progressively through all seasons during the turtles' first 3 years of life. Afterwards, densities were always lower in winter but increased in summer. The data for trematodes in *C. picta* are less obvious, but the same trend is apparent. In South Carolina, however, the nematode *Camallanus trispinosus* (also present in Michigan *C. picta*) overwintered in hibernating *T. scripta*; this was followed by losses in mid- to late summer. *Spironoura chelydrae*, also a nematode, appeared to decline during the period of hibernation and was then rapidly recruited in early spring (Esch et al., 1979a).

The pattern of seasonal change for *Neoechinorhynchus* spp. appears to be more complicated than that for nematodes in *T. scripta* (Esch et al., 1979a). At least two waves of infection (in May and July) were observed. From February to May, larger worms became more abundant. In May, densities and prevalence of larger worms sharply declined, and there was an equal increase in small individuals. Another cohort of smaller worms appeared in July. Esch et al. (1979a) also observed that the greatest mortality of acanthocephalans either shortly preceded or occurred simultaneously with parasite recruitment.

Dubinina (1949) indicated that young nematodes of *Testudo horsefieldii* continued to mature at a slow rate during hibernation, but older ones died early during the period. It is apparent from her work and that of Esch and Gibbons (1967) and Esch et al. (1979a) that hibernation does not always lead to parasite mortality and that seasonal change in parasite density in many cases appears to be a species-specific phenomenon. The seasonal change is probably linked to the seasonal dynamics of potential intermediate hosts, to changes in host feeding patterns, or to other factors such as the host's immune responsiveness, which in some poikilotherms can be influenced greatly by temperature extremes, both high and low (Esch et al., 1975).

HABITAT

The nature and quality of the habitat may greatly affect infrapopulation densities as well as the structure and dynamics of parasite infracommunities in turtles. This generalization is well illustrated by comparing the trematode and acanthocephalan faunas in Wintergreen Lake *C. picta* (Esch and Gibbons, 1967) with those of *T. scripta* from the SRP (Esch et al., 1979a,b). Eight species of enteric trematodes infect *C. picta* in Michigan. Only two, possibly three, species occur in *T. scripta* from South Carolina.

Trematodes dominate the overall parasite fauna in numbers of species in Michigan. In South Carolina the helminth fauna is dominated numerically by acanthocephalans. Because all trematodes require mollusks as their first intermediate hosts, the best explanation for these differences is related to the richness of the Michigan molluscan fauna, which is low in species diversity in South Carolina (Esch and Gibbons, 1967). This is probably a consequence of the relatively high pH and high calcium content of Michigan waters versus the comparatively lower pH and low calcium levels in South Carolina waters. Differences in the acanthocephalan faunas in Wintergreen Lake and the SRP are striking. Rather than being due to physiographic characteristics associated with the two areas in question, the differences are probably due to the absence of appropriate intermediate hosts in Wintergreen Lake. This assertion is based on an anecdotal observation (by Esch) of *Neoechinorhynchus* sp. in a box turtle captured in close proximity to the Wintergreen Lake shoreline. Certainly the opportunity for establishing *Neoechinorhynchus* in Wintergreen Lake exists.

Although only a single habitat was sampled in the Michigan study, a series of habitats was sampled on the SRP (Esch et al., 1979a,b). These habitats included sites that were currently receiving thermal effluent from several nuclear production reactors or that had received it and were in postthermal recovery and sites that had never been affected by thermal perturbation. Also included were streams, small farm ponds, a river swamp, and a large reservoir. In general, the results of comparing parasite infracommunity diversity in turtles from a wide range of habitats on the SRP indicate that parasite heterogeneity among the habitats is also wide. Parasite diversity appeared to be related to habitat stability. For example, the river swamp habitat had the most diverse helminth fauna; a small cooling pond that received large volumes of thermal effluent had the least diversity. The highest infracommunity diversity and species numbers were in turtles from stable habitats, whereas the lowest diversity and species numbers were from turtles in habitats subjected to perturbation or to the vagaries of natural environmental change such as irregular rainfall. These findings, according to Esch et al. (1979b), tend to support the time-stability hypothesis of Sanders (1968), which suggested that low species diversity may be a function of either severe or unpredictable environmental conditions.

Slobodkin (1967) suggested that the response of an individual organism to noncatastrophic perturbation will be an increase or a decrease in survival probability, a change in fecundity, or both. Any of these sorts of change would lead to alterations in the population biology of the organisms in question. According to Esch et al. (1975), environmental perturbations that produce ecosystem stress will inevitably lead to modification in host-parasite

interactions, which in turn may lead to local extinction of hosts, parasites, or both. The studies by Eure and Esch (1974), Eure (1976), and Esch et al. (1979a,b) tend to support this prediction regarding the nature of change in host-parasite interactions within stressed or otherwise unpredictable habitats.

PATTERNS IN HELMINTH COMMUNITIES

As Holmes and Price (1986) pointed out, the challenge is to determine the factors that lead to a given position on the isolationist-interactive continuum. Recently, Kennedy et al. (1986) identified several factors that lead to establishment of isolationist or interactive helminth infracommunities, by comparing helminth infracommunities from piscine and avian hosts. They concluded that at least five factors were important in creating potentially interactive infracommunities: high host vagility, endothermy and complex alimentary canal, a broad host diet, selective feeding by the host on prey serving as intermediate hosts for a wide variety of helminths, and exposure to direct-life-cycle helminths. It is valuable to examine the extent to which turtle helminth systems fit these generalizations. Although diversity indexes are not available for individual turtle helminth infracommunities, we can make predictions based on presence-absence data from parasite survey data of selected turtles (Ernst and Ernst, 1977) of varying ecologies to test these concepts at the component level. The concepts at this level of helminth community organization focus on the factors that determine the helminth species richness in a host species (Holmes and Price, 1986).

Kennedy et al. (1986) reasoned that hosts with complex enteric systems would offer greater opportunity for helminth colonization and species diversity than hosts with simpler gut physiology. Reptiles are intermediate between amphibians and birds in terms of their gut complexity, being the first vertebrates in which true colic ceca are found (Weichert, 1970). Thus, based on this feature, we would predict that turtles would lie on an intermediate position on the isolationist-interactive continuum.

Intestinal complexity is related to endothermy. Birds and mammals, in maintaining endothermy, have greater metabolic demands than do fish and amphibians. As a consequence of their more vigorous feeding regimes, endotherms are more likely to be exposed to a greater variety of helminths than are ectotherms. Although reptiles generally cannot generate their own body heat, basking is an important thermoregulatory behavior, especially among turtles, in which atmospheric basking causes a rise in body temperature (Boyer, 1965; Crawford et al., 1983). This phenomenon would have important implications for the parasite fauna of turtles. Increased body temperatures would result in increased feeding, exposing turtles to a greater

variety of helminths transmitted as a consequence of host feeding patterns. We would predict that behaviorally thermoregulating hosts would be positioned at an intermediate location on the isolationist-interactive continuum.

Host vagility (movement through varied habitat types) plays an important role in influencing helminth species richness in hosts. The available data indicate that many chelonians are quite vagile. The most spectacular cases are those of many marine turtles, the females of which migrate hundreds of miles from their feeding grounds to nest (Carr, 1965). Freshwater turtles are also vagile. Indeed, the different reproductive strategies of the two sexes in several species of turtles are primary factors influencing differential activity and movement of turtles (e.g., Morreale et al., 1984). Long-range movements of nesting females as well as mate-seeking behaviors of male turtles have been described (for a review, see Gibbons, 1986). For example, males of *T. scripta* move extensively over long distances in search of mating opportunities (Morreale et al., 1984). We predict that such vagility would expose turtles to a wide range of potential intermediate hosts as well as to encysted stages of parasites on vegetation and species with direct life cycles.

As we have mentioned throughout our discussion, host feeding patterns are a critical factor affecting species richness of helminth infracommunities. Turtles with a broad host diet would be expected to harbor more speciose helminth faunas than turtles that are dietary specialists. For example, more parasite species have been described from semiaquatic emydid turtles (e.g., *Chrysemys*, *Trachemys*) than from turtles that are more terrestrial (e.g., *Kinosternon*, *Gopherus*, *Terrapene*). Helminth faunas of terrestrial turtles are dominated by nematodes, many of which have direct life cycles. Kinosternid and testudinid turtles are less likely to be exposed to parasites whose life cycles rely upon host feeding habits for transmission. Emydid turtles, being omnivorous, are exposed to significantly more parasites. For example, the rich acanthocephalan fauna transmitted as a function of herbivory in *T. scripta* (Esch et al., 1979a) is a result of accidental ingestion of ostracods, which are intermediate hosts and are associated with the vegetation on which *T. scripta* feeds. This supports the fourth prediction of Kennedy et al. (1986), which suggests that feeding on prey that serve as intermediate hosts for a variety of helminths would enhance species diversity. In turtles, dietary and habitat shifts are associated with host size (e.g., Hart, 1983). Because helminth colonization is largely a function of turtle feeding patterns, knowledge of the life cycles of the parasites present provides valuable information for the turtle ecologist wishing to understand the nature of such shifts.

Because of evolutionary factors and certain characteristics discussed above, turtle helminth communities should show diversity values intermediate between those of fish

and birds. Moreover, based on the above characteristics, some turtle species should harbor abundant populations of certain helminths. These features should be reflected in an intermediate position on the isolationist-interactive continuum proposed by Holmes and Price (1986). Our predictions are supported by diversity analysis and helminth abundance data of individual infracommunities of *T. scripta* (Esch and Gibbons, 1967; Esch et al., 1979a; Jacobson, 1987). Application of the Brillouin's diversity index to individual infracommunities of *T. scripta* revealed that they are, indeed, intermediate between the fish and avian infracommunities studied by Kennedy et al. (1986).

It is at the infracommunity level that any direct interactions between parasites must take place, and it is at this level that evidence for interactions must be examined (Bush and Holmes, 1986). The significance of biotic interactions in helminth communities depends on characteristics of the component community discussed above. That is, interactions between helminth species should be common only if parasites exist at high intensities within the host. Clearly, this is feasible for some turtle species. We examine the potential for helminth interactions by comparing two turtle species that support abundant populations of enteric congeneric parasites.

A study of the infracommunity structure of enteric helminths in *T. scripta* has recently been completed (Jacobson, 1987). The procedure of Bush and Holmes (1986) was used to examine the nature of helminth organization within the intestine. It involves removing the intestine and freezing it instantly in dry ice and ethanol to prevent postmortem migration of helminths. The intestines can then be stored until examination, upon which they are measured and cut into 20 equal sections. Each section is then examined for parasites, and their location is expressed as a percentage of the intestinal length. In some turtles the precise location of a parasite was determined relative to others of the same and different species.

A large component (four species) of the helminth fauna of *T. scripta* consists of acanthocephalans of the genus *Neoechinorhynchus*. These are largely responsible for the diversity values mentioned above. Preliminary evidence reveals that these acanthocephalan species are sympatric in both their linear and their circumferential distributions. That is, it appears that the presence of one acanthocephalan species has little or no effect upon the location of another species. The noted patterns of co-occurrence suggest that competitive interactions are not important in structuring the infracommunities of *T. scripta*.

In marked contrast to the above study is the investigation of Schad (1963), who studied the infracommunity structure of the nematode fauna of the European tortoise *Testudo graeca*. An important feature of this host's fauna is that it consists of 10 congeneric species of the nematode *Tachygonetria*, all residing in the colon. Schad's initial ob-

servations indicated a significant overlap in the linear distribution of the 10 species, suggesting that they were capable of sharing the spatial resources within the colon. However, when he examined their radial distributions, he found the linear overlapping to be of little consequence. Using colons that had been quickly frozen at -147°C in liquid air, he was able to establish that several species showed a strong preference for the paramucosal lumen, whereas others were scattered in the lumen away from the mucosal area. Then, based on an analysis of the oral morphology and food habits of two species of overlapping nematodes, Schad was able to determine that one was an indiscriminant feeder on lumen contents, whereas the other fed exclusively on bacteria. He also observed striking dissimilarities in the oral morphology of other species combinations having similar distribution patterns and concluded that they probably also differed in food preferences. It is possible that this community was structured by historical competitive interactions with the development of resource partitioning among the nematodes.

Prospects for Future Study

Future investigations of the biology and ecology of turtle parasites should fall into three separate and distinct categories. The first is to use turtle parasites for developing a better understanding of the biogeographical distribution of American turtles belonging to the family Emydidae. As was noted earlier, a unique aspect of many host-parasite relationships is the phenomenon of strict host specificity, and such specificity generally implies a long association between host and parasite. More important, it means that certain parasite species within an infracommunity can be used as tags, or markers, and, as such, may be useful in assessing the radiation of the host species. For example, Barus and Moravec (1967) were able to identify seven species of helminth parasites from *Trachemys decussata* on the island of Cuba. Of these, five had been previously described by Harwood (1932) from emydid turtles in Texas. The same five were also identical to species recovered by Rausch (1947) from emydid turtles in Ohio, close to the northernmost geographic limits of these hosts. Because turtles of the genus *Trachemys* are scattered over many of the Caribbean islands and on the Western Hemisphere mainland down to South America, it would be possible to use their parasite faunas to study the biogeographical radiation of turtles from the southern United States into the northwestern, north central, and eastern United States as well as down into Central and South America. Such studies would also permit evaluation of the nature and extent of parasite exchange or transfer among closely related, or even distantly related, species of turtles, fish, and amphibians. A broad biogeographic approach such as that adopted by Price

and Clancy (1983), when applied to turtles, would be of great interest in interpreting patterns and processes important in the structure and dynamics of helminth communities. Finally, it is conceivable that the study of emydid turtles in isolated areas of Central and South America, as well as on various Caribbean islands, might allow for the determination of the rate of evolutionary change that has occurred within infracommunities of relict host populations.

A second area for potential study is the intrapopulation dynamics of parasites in turtles from a range of habitats. Esch et al. (1979a,b) have clearly shown that parasite intrapopulation dynamics vary according to habitat stability. The precise mechanisms affecting this variability are, however, unclear. An understanding of these mechanisms would be useful in obtaining comparative informa-

tion relative to parasite population biology among hosts of different taxa in aquatic ecosystems.

Finally, we feel confident that additional knowledge regarding the basic biology of turtle parasites will contribute to a better understanding of the biology and ecology of the turtles themselves. Furthermore, such information will be useful in comparing similar phenomena among various freshwater vertebrate taxa, ranging from fish to amphibians and other turtles.

Acknowledgments

Research and manuscript preparation were made possible by contract DE-AC09-76SROO-819 between the University of Georgia and the U.S. Department of Energy and by National Science Foundation grant DEB-79-04758.