

THE GREEN SALAMANDER (*ANEIDES AENEUS*) IN TENNESSEE AND KENTUCKY, WITH COMMENTS ON THE CAROLINAS' BLUE RIDGE POPULATIONS

DAVID H. SNYDER

*The Center for Field Biology and Department of Biology
Austin Peay State University
Clarksville, TN 37044*

ABSTRACT

Most populations of the green salamander (*Aneides aeneus*) occur primarily on the southern half of the Appalachian Plateau Geologic Province from southwestern Pennsylvania to northeastern Mississippi. A distinctly disjunct group of populations is on the southern end of the Blue Ridge Geologic Province in southwestern North Carolina and adjacent parts of South Carolina and Georgia. In the late 1970s the Blue Ridge populations crashed severely, while the Appalachian Plateau populations apparently did not. In an attempt to assess more accurately the status of the Tennessee and Kentucky populations during that period, data were collected from 1) a survey of field workers who had field experience with *Aneides aeneus* in those two states during the critical period, 2) the files of three governmental inventory projects, and 3) the published literature. These data indicate that *Aneides aeneus* populations in Tennessee and Kentucky did not crash severely during the late 1970s. Some possible reasons for the crash of the Blue Ridge populations are discussed, and a plea is made for long-term monitoring of selected bioindicator species, possibly to include *Aneides aeneus*.

INTRODUCTION

The green salamander, *Aneides aeneus*, occurs primarily on the southwestern half of the Appalachian Plateau Geologic Province, from extreme southwestern Pennsylvania to extreme northeastern Mississippi (Conant and Collins 1991). In Kentucky *A. aeneus* is restricted to the Appalachian Plateau, but in Tennessee its range extends west slightly onto the Interior Low Plateaus, and east onto the Ridge and Valley. A distinctly disjunct group of populations occurs in several counties in southwestern North Carolina, extreme northwestern South Carolina, and extreme northeastern Georgia, at the southern end of the Blue Ridge Geologic Province (geologic provinces based on Shimer 1972).

Our knowledge of the life history of *A. aeneus* is based largely on the studies of Gordon (1952), Woods (1968), Snyder (1971), and Cupp (1991). Gordon and Snyder worked with the Blue Ridge populations. Woods studied a population at the extreme southwestern terminus of the Appalachians (and of the species' range), in Tishomingo County, Mississippi. Cupp's work has been conducted primarily in southeastern Kentucky, near the center of the species' range.

Aneides aeneus is a habitat specialist, as a scansorial rock- face and crevice dweller. Typically this species occurs on noncalcareous sandstone substrates, especially the Pottsville sandstone (Gentry 1955). It also occurs on granites and schists in the Blue Ridge, and has occasionally been reported from limestones (but usually near sandstones in such cases). Congeners in the western United States are highly arboreal, and though there are reports of *A. aeneus* occurring on or in trees (Barbour 1971, Gordon 1967, Gentry 1955), either standing or down,

such habitats are surely not the typical situation over most of its range today.

At night and sometimes on cloudy days *A. aeneus* may be seen foraging over exposed rock faces. The rock faces must be protected from prolonged exposure to the direct sun, by either aspect or vegetation shading. But for daytime retreats, brood chambers, and hibernacula, appropriate crevices in the rocks are needed. These crevices must be moist but not wet, and relatively clean; the species shuns crevices with dirt on the floor, though a few rootlets and light overgrowths of mosses or lichens may be tolerated (pers. obs., Gordon 1952).

Though *A. aeneus* has a moderately extensive geographic range for a plethodontid salamander of the eastern U.S., its need for suitable rock substrates results in a very spotty distribution even in areas where it is known to occur. It is rarely seen on the forest floor far from suitable rock outcrops, or on blacktop road surfaces on rainy nights when many other salamander species may be found in large numbers (an exception to this was discussed by Williams and Gordon 1961). Because of its strict microhabitat requirements it is relatively inconspicuous to field workers not aware of those requirements; generalized herpetological collecting techniques, such as log rolling, stone turning, duff raking, streambank cruising, and nightlighting of the forest floor may well yield few or no *A. aeneus*, even in the vicinity of substantial populations (pers. obs.).

The question of gene flow among populations occurring on different and isolated rock outcrops has not been studied, though no subspecies have been described.

The Crash of the Blue Ridge Populations

In 1970 I worked with several southern Blue Ridge populations of *A. aeneus* from April through October. During that time I visited populations in several counties on a weekly schedule while investigating brooding behavior in the species (Snyder 1971). Altogether I found more than 200 clutches of *A. aeneus* eggs. Assuming a one-to-one sex ratio, and that the females produce eggs on a biennial schedule, then those 200 clutches bespeak an adult population of about 800 individuals; assuming further that I detected half the clutches actually present on the rock outcrops I worked, the estimate of adults becomes 1600; if half the individuals in those populations were juveniles or subadults, the estimate of total population rises to 3200. Though these calculations invoke some unverified assumptions regarding the demographic features of the populations, detectability of the egg clutches, etc., I believe the assumptions are reasonable and that the estimate of 3200 individuals present in these populations is conservative. At least the finding of 200 egg clutches is evidence that the populations of *A. aeneus* in the Blue Ridge were robust in 1970.

Since 1970 I have returned to the southern Blue Ridge about 15 times, usually checking on some of the more accessible *A. aeneus* populations I worked in 1970. By the late 1970s it was becoming quite

difficult to find *A. aeneus* at sites which had previously harbored many individuals. By August 1982, at the Second Decennial Symposium on the Biology of Plethodontid Salamanders, convened at Highlands Biological Station, it had become obvious to Richard Bruce, Director of the Highlands Biological Station, that the local *A. aeneus* populations had crashed. Though no systematic monitoring program was in place to provide quantitative data upon which to base such a conclusion, the anecdotal comments of several salamander experts at the symposium, plus comments that Bruce had been hearing from field workers in recent years, plus Bruce's own experience, made the conclusion inescapable. Immediately after that symposium Jack Sites and I spent an afternoon looking for *A. aeneus* at the richest site I had worked in 1970, but found none. In April 1983, at the annual meeting of the Association of Southeastern Biologists, I reported on the crash of the Blue Ridge populations (Snyder 1983).

In August of 1983 I spent four days looking for *A. aeneus* at most of the sites I had worked in 1970, without success. Those sites not checked in August were checked in October of the same year, and on that trip, at the Lower Whitewater Falls site (at 488 m this was the lowest site I had worked in 1970), I found four individuals: three hatchlings (probably not yet dispersed from their natal crevice), and a subadult about two inches snout-vent length.

In 1990 the North Carolina populations of *A. aeneus* were placed on that state's list of endangered species by the North Carolina Wildlife Resources Commission.

Reason for this Study

At the First World Congress on Herpetology, held in Canterbury, England in September 1989, it became apparent, through casual conversations among several of those in attendance, that amphibian populations representing many species from diverse parts of the world have experienced severe population declines. Populations occurring in pristine areas have not been exempt. Though the evidence for the declines was mostly anecdotal, or only crudely quantitative, it was convincing enough to arouse serious concern among many of those present. David Wake of the University of California at Berkeley convened a two-day workshop on the problem during the following February, under the sponsorship of the National Research Council's Board on Biology (Phillips 1990). As a result of that workshop, a special one-day informational symposium was organized in conjunction with the regular annual meeting of the Society for the Study of Amphibians and Reptiles, and The Herpetologists' League, held at Tulane University in New Orleans in early August, 1990. That symposium was titled "Global crisis in declining amphibian diversity: analyses of critical components." More than two dozen researchers from across the Western Hemisphere and Australia made presentations. By the end of the day two things were apparent: the problem was geographically extensive and locally intensive; and the kinds and amounts of data needed to quantify and explain the declines were, almost without exception, not available.

That symposium caused me to think anew about the recent history of the *A. aeneus* populations in the Blue Ridge. How does that situation fit into the larger picture which emerged at the symposium? What was happening to *A. aeneus* in Kentucky and Tennessee, at the heart of the species' range, during the years when the Blue Ridge populations were crashing? Given the suitability of amphibians generally as bioindicators of chemical pollution of the environment, might *A. aeneus* be an especially good candidate for a long-term monitoring program of its population fluctuations and ecophysiology? The major purpose of this paper, then, is to present what evidence is available regarding the status of the *A. aeneus* populations in Kentucky and

Tennessee during the last 20 years or so, to compare that status with what we know happened to the Blue Ridge populations during the same period (as outlined above), to discuss some possible reasons for the crash of the Carolinas' populations, and to consider the prospect of *A. aeneus* as a good bioindicator species for assessing environmental quality.

METHODS

Information on the distribution and status of *A. aeneus* populations in Kentucky and Tennessee for the past 20 years (and more in some cases) was gathered from several sources including: (1) a survey of field workers who may have had experience with *A. aeneus* in those two states during the specified period, (2) data files of state and federal organizations, and (3) the published literature.

Survey of Field Workers

I contacted (by telephone in most cases) 12 people who I suspected might have had field experience with *A. aeneus* in Kentucky or Tennessee in the last 20 years. They were asked for their general impressions of *A. aeneus* populations encountered in the field in either of those two states during the last 20 years, or however long was appropriate in their particular case. Such data of course have real limitations and must be interpreted judiciously, but it seemed reasonable to assume that if widespread, major trends had occurred, then a distillation of the responses to such a query should reflect those trends. The extent of field experience with *A. aeneus* varied widely among the several respondents, but without exception they were sympathetic with my purpose, and cooperative. In fairness to them, considering the informal nature of the survey, their responses reported below are anonymous.

Data Files of State and Federal Organizations

The Kentucky Natural Heritage Program of the Kentucky State Nature Preserves Commission, the Regional Heritage Inventory Project of the Tennessee Valley Authority, and the Natural Heritage Program of the Ecological Services Division of the Tennessee Department of Conservation all provided me with their occurrence records of *A. aeneus*. These files provide the best quantitative data available on the status of *A. aeneus* populations in their respective geographic areas of concern over the past several decades, though even in this case the records are largely anecdotal. The files of these organizations are based on published literature, unpublished in-house reports, museum records, personal contacts with knowledgeable biologists, and field reconnaissance by their own personnel. Though the data in these files are far from ideal for the purpose of detecting population trends in the species included, they are not always useless for that purpose, at least for some species and at a coarse level of resolution; surely a population crash to near extinction, as occurred in the Blue Ridge populations of *A. aeneus* in the late 1970s, should be reflected in such files. The value of these files can only appreciate with the passage of time and the continuous addition of new records.

RESULTS

Survey of Field Workers

Of the 12 people I surveyed, five had no impressions of *A. aeneus* population trends in Kentucky and Tennessee during the last 20 years because of very limited field effort targeted at this habitat specialist. But seven respondents did have impressions based on a significant amount of field effort. One reported that a substantial population of *A. aeneus* existed at Bays Mountain State Park in Hawkins County, Tennessee, some five to ten years ago. Another reported having seen *A. aeneus* as recently as five years ago on the lower slopes of Signal

Mountain in western Hamilton County, Tennessee, not far from downtown Chattanooga in what must be some of the most polluted air in the state. In Kentucky, a respondent who has been visiting *A. aeneus* habitat in that state for the last 20 years (while searching for other species which also occur in such habitat) has no impression of any decline in the species there during that period. Two workers in East Tennessee reported vague impressions that some *A. aeneus* populations they have visited intermittently in that area were down somewhat between the early- and mid-1980s. A respondent who has worked Kentucky *A. aeneus* populations regularly over the past 20 years reported the distinct impression that they were down significantly in the late 1970s and early 1980s, but have recovered well since then. Another person reported from Kentucky his impression that *A. aeneus* at the sites he has worked for more than 15 years are probably doing all right, though possibly down a little in recent years; he stressed the wide variation in *A. aeneus*-detections-per-unit-search-effort he has obtained, during both daytime and nighttime visits to sites, both among years and among visits during the same year.

Data Files of State and Federal Organizations

Table 1 presents a summary of *A. aeneus* records in the files of the Kentucky Natural Heritage Program and the Tennessee Valley Authority's Regional Heritage Inventory Project, by five-year intervals, from 1950 through 1989. In the case of the TVA data, records of *A. aeneus* from the Blue Ridge portion of its range are listed separately as the second row of figures in the table. Though the amount of field effort behind these data is not controlled for, it is nonetheless apparent that *A. aeneus* populations did not crash to near extinction after 1975

Table 1. Numbers of individuals or individual egg clutches of *Aneides aeneus* represented in the data files of three heritage programs 1950-1989, (by five-year intervals), from the main Appalachian Plateau populations and the disjunct Blue Ridge populations.

Populations	Years							
	1950-1954	1955-1959	1960-1964	1965-1969	1970-1974	1975-1979	1980-1984	1985-1989
Applchn. Plateau	14	7	41	58	15	21	64	75
Blue Ridge	4	8	29	13	141	0	0	0

in the main portion of their range (the Appalachian Plateau populations, line one in the table). Significantly, the data from the Blue Ridge portion of *A. aeneus*' range (line two in the table) reflect what I know to be true from extensive personal experience with the Blue Ridge populations—namely that those populations crashed hard in the late 1970s.

Literature reports

Data in the published literature on the size of *A. aeneus* populations in Kentucky and Tennessee during the last 20 years are almost nonexistent. Redmond (1985) summarized our knowledge of the geographic range of *A. aeneus* in Tennessee as of that date, but said nothing of

population sizes or fluctuations. In Kentucky, Barbour (1971), commenting on conditions there before 1970, stated that the species was "particularly abundant in areas of sandstone outcroppings," and remarked that "They reached tremendous populations in the 1930s under the bark of the millions of dead chestnut trees in eastern Kentucky."

DISCUSSION AND CONCLUSIONS

Possible Reasons for the Crash of the Carolinas' Populations

Though the cause of the crash of the Blue Ridge *A. aeneus* populations is obscure, speculations have abounded. It may be that the crash was a natural but chaotic effect caused by deterministic processes exhibiting sensitive dependence on initial demographic conditions and life history parameters, and not caused by any environmental factor. The list of possible environmentally correlated causes included acid precipitation, disease, predation (including over-collecting by herpetologists), habitat destruction, and adverse weather.

May (1976a, 1976b) described how wildly irregular (chaotic) fluctuations in animal population sizes may predictably result from even simple deterministic equations describing the dynamic trajectories of such populations. As May (1976a) put it, "apparently erratic fluctuations in the census data for animal populations need not necessarily betoken either the vagaries of an unpredictable environment or sampling errors: they may simply derive from a rigidly deterministic population growth relationship...." This idea, so discomfiting to many classically trained ecologists and population biologists, has been termed "The Butterfly Effect" (Gleick 1987). The importance of the phenomenon in actually explaining real life "booms" and "crashes" of populations is still, 15 years after the appearance of May's two seminal papers, nearly impossible to assess in particular cases. This is true because of our profound ignorance regarding both the appropriate population growth equations we should be using in particular instances, and the parametric values that should be employed in those equations. But the intuitive lesson is clear: environmental correlates may not exist for some population booms and crashes.

For various reasons, several of the environmental-agent suggestions seemed implausible to me. Catastrophic epidemic disease seemed unlikely given the general resistance of salamanders—or at least the absence of evidence of their susceptibility—to such diseases, and given also the degree of isolation of several of the populations.

Predation by a non-human predator seemed unlikely and predation by humans (in the form of over-collecting by herpetologists) seemed an equally improbable cause. Although human predation may devastate local populations, several of the populations I worked in 1970 were quite remote and not easily accessible—some of these I discovered myself and I am fairly confident were known only to me—yet they crashed. Habitat destruction has definitely decimated some *A. aeneus* populations, or at least caused the animals to evacuate some sites; removal or opening up of the shading canopy is all that is needed, and that of course commonly happens when an area is cleared or "thinned out" for construction purposes. I know of sites around Highlands, North Carolina, where just that thing has happened and it will be decades at least before the canopy can close again sufficiently to provide adequate shade for *A. aeneus* to recolonize the exposed rock faces. But again, such local disturbances cannot account for the are-wide crash of the populations that occurred in the remotest, undisturbed, and possibly even unvisited (by anyone but me) sites.

Acid precipitation and unusually severe weather seem to be the most plausible catastrophic agents from the aforementioned list of possible environmental causes. The last 20 years have witnessed a growing concern among environmentalists over the effects of acid precipitation on natural ecosystems. Though a significant literature

exists on the question of the effects of acid deposition on amphibians (e.g., Hutchison et al. 1980, Wyman et al. 1987, Pierce 1985), most of it concerns aquatic systems and the associated stages of amphibian life cycles. Ireland (1991) has recently reported that not only must the hydrogen ion be considered when assessing the effects of environmental acidification on amphibians (he assessed the growth of larval *Ambystoma maculatum*), but also acid-derived anions. But it has proven difficult in field situations to ascribe with certainty particular instances of environmental change (including declines of amphibian populations) to increases in the acidity of atmospheric precipitation. As Pierce (1985) understated the situation, "additional research is needed to predict the full range of effects acidity may have on [amphibian] populations."

In the specific case of the Blue Ridge *A. aeneus* population crash of the late 1970s and early 1980s, I believe the weight of the evidence is against acid precipitation as the probable cause. It is true that the Blue Ridge *A. aeneus* populations occur on geologic substrates that result in generally inferior acid buffering capacities compared to substrates throughout the main part of the species' range (see the map in Likens et al. 1979). It is true also that the acidity of precipitation in the region increased dramatically from 1956 to 1976 (Likens et al. 1979). Given these facts, and considering that *A. aeneus*—unlike many of the salamanders sympatric with it—spends most of its time on rock substrates rather than on soil, duff, or vegetation (and would therefore likely be more directly exposed to rain before its acidic properties were affected by contact with neutralizing substrates), and that as an amphibian *A. aeneus* has very permeable skin (thus enhancing its susceptibility to ionic exchange with its environment), it initially seemed likely that increased acidity of the precipitation in the area was a good candidate for the cause of the population crash. However, the Blue Ridge *A. aeneus* populations have been recovering in recent years (pers. obs.; Richard Bruce 1990, pers. comm.; Jeffrey Corser 1990, pers. comm.), and this recovery is occurring in the face of no significant decrease in the acidity of precipitation during that period.

That leaves factors associated with severe weather, especially drought and cold, as possible environmental causes, at least among those mentioned above. Though, of all terrestrial vertebrates, amphibians are generally the most susceptible to drought stress (because of their water-permeable skins), I believe that drought is unlikely to have caused the widespread and catastrophic crash of the Blue Ridge *A. aeneus* populations which apparently affected all age classes. I (Snyder 1971) observed an increased rate of clutch loss in *A. aeneus* during a three-week drought in 1970, but too few nests were involved to allow for a test of statistical significance; however, the attending female is not known to have succumbed with any of those clutches lost during that drought. All members of an *A. aeneus* population (except, possibly, brooding females) would appear to have the option during a drought of simply retreating to microhabitats wherein water loss was a manageable problem, though it is at least conceivable that a drought could be so prolonged and so severe as to eliminate such microhabitats. There were some unusual droughts in the southern Blue Ridge during the period in question, and it is just conceivable that they eliminated all safe refuges in spite of the ability of *A. aeneus* to move during warm weather.

There were also some winters in the late 1970s which produced unusually low temperatures that persisted for unusually long periods. Such conditions could have "caught" many or most of the hibernating *A. aeneus* in a torpid condition in their winter retreats which were safe havens during the less severe and less prolonged cold snaps of a normal winter. Unable to rouse from their torpor to move into deeper and warmer recesses of their hibernacula (ahead of the advancing frost

line), they would have frozen. Only those individuals which had initially hibernated deep enough in the crevices to have escaped the unusually deep frost lines of those abnormally severe cold spells would have survived to launch a recovery of the population, as is apparently occurring today. Heyer et al. (1988) reported on what may have been a similar event involving the local extinction of several populations of frogs in southeastern Brazil caused by unusually heavy frosts in 1979; in the case of some of the species, common before 1979, not a single individual had been seen in the area affected—in spite of diligent attempts to find them—as recently as 1984.

The scenario presented in the preceding paragraph as an explanation for the crash of the Blue Ridge *A. aeneus* populations in the late 1970s seems plausible, given what we know of that situation. But I must emphasize the tentative nature of such an explanation. We do not know how deeply *A. aeneus* retreats into its hibernacula during winter in the Blue Ridge, or how deeply the frost line penetrated into those hibernacula during those severe winters. If this explanation is indeed the correct one, an obvious question is why didn't the *A. aeneus* populations in the main part of the species' range (the southern Appalachian Plateau) suffer a similar fate? After all, those severe winters were not restricted to the Blue Ridge. It may be that the Appalachian Plateau populations hibernate deeper in their retreats, either because of the greater availability of such deep recesses, or because of genetically-based behavioral differences between the two groups of populations. It may also be relevant that the elevations of the populations I worked in the southern Blue Ridge (13 sites, mean elevation = 952 m) averaged considerably above the elevations of *A. aeneus* populations on the southern Appalachian Plateau; that extra altitude is likely to have been correlated with significantly lower temperatures during the cold snaps.

Aneides aeneus as a Bioindicator of Environmental Quality

The data presented in the preceding section indicate that *A. aeneus* populations in Tennessee and Kentucky did not crash severely in the late 1970s and early 1980s.

The data, which I believe to be the best available on the question, also emphasize the inadequacy of our present system (or nonsystem) of monitoring population trends in most nongame species. We could do much better with some planning and central coordination of effort.

I am not sure what governmental agency or agencies should be responsible for that planning, or what the administrative flow chart should look like; that question is one for the agencies themselves to address and solve. But to the extent that the various governmental units have an interest in and responsibility for the monitoring and maintenance of nongame wildlife populations, they should cooperate among themselves in establishing a long-term program, geographically and taxonomically broad in its scope.

A list of target species should be compiled whose monitoring would serve to track the overall "health" of an ecosystem. Many factors should affect the selection of a constellation of such "vital species" for monitoring in any particular ecoregion. Ecologists, ecological physiologists, population biologists, taxonomists, and land managers should all have input into compiling such a list.

Examples of factors that should be considered in selecting a list of "vital species" are: (1) what kind/s of environmental degradation is the species especially susceptible to? (2) are the ranges of tolerance of the species to particular ecological insults so wide or so narrow that they make it a poor choice as a "vital species"? (3) what is the species' position in the food pyramid, and what bearing does that position have on the bioconcentration of toxic chemicals and their metabolites in the organism's tissues? (4) how extensive is the geographic range of the

species, and how distinctive is the ecoregion represented? (5) what is the nature of the species' physiological exposure to its environment (e.g., is the species aquatic or terrestrial or both, and is its skin relatively permeable or impermeable to ion exchange with its medium or substrate)? (6) how easy is the species to "census" (or at least index) in the field (e.g., is it common or rare, secretive or not secretive, accessible or inaccessible)? and (7) how extensive is the database already available for answering the questions posed above?

The foregoing list is only exemplary, and doubtless needs refining. But it at least indicates some of the kinds of things that must be considered when selecting a list of species, some populations of which are to be monitored on a long-term basis as an assessment of ecosystem health.

A. aeneus is a good candidate for such a list, for the following reasons: (1) as an amphibian, it has—by virtue of its permeable skin—an unusually intimate physiological interaction with its environment; (2) because it is exclusively terrestrial it is not much affected by problems of aquatic pollution; (3) its moderately extensive geographic range insulates it against localized catastrophes, and yet bespeaks a species whose environmental tolerances are not so broad as to render the species immune to all but the most vigorous environmental insults; (4) its limited contact with the forest floor (and its accumulated duff) may mean that *A. aeneus* is more directly exposed to unadulterated acid precipitation than are other, sympatric amphibians; (5) as a long-lived carnivore, it should exhibit bioconcentration of toxicants in its environment; and (6) its microhabitat preferences (rock crevices) make it easy to monitor populations on a regular basis with no more disturbance to the animals than that caused by shining a light on them, and with assurance that the exact same crevices can be checked during each monitoring episode, thus rigorously standardizing the censusing effort.

In the Blue Ridge portion of *A. aeneus*' range a long-term monitoring program is being instituted this year, under the sponsorship of the U.S. Forest Service and Highlands Biological Station. A specific site for that project has already been selected, and censusing protocol and other details of the project are now being finalized. In view of the disparate recent histories of the populations of *A. aeneus* in the Blue Ridge and the main Appalachian Plateau portion of its range, now seems an auspicious time to institute a similar program at some site (or sites) in Tennessee and Kentucky.

ACKNOWLEDGMENTS

I thank the field biologists who shared with me their impressions of *Aneides aeneus* populations in Tennessee and Kentucky during the last 20 years. Rich Hannah (Kentucky Natural Heritage Program, Kentucky State Nature Preserves Commission), Bill Redmond (Regional Heritage Inventory Project, Tennessee Valley Authority), and

Paul Hamel (Natural Heritage Program, Ecological Services Division, Tennessee Department of Conservation) all kindly provided me with occurrence records of *A. aeneus* in their respective data files. Dick Bruce (Highlands Biological Station) has been a confidant for many years in matters regarding the status and plight of the Blue Ridge *A. aeneus* populations, and I am indebted to him for his observations and thoughts on the subject. Floyd Scott and an anonymous reviewer made several helpful suggestions on the manuscript.

LITERATURE CITED

- Barbour, R. W. 1971. Amphibians and reptiles of Kentucky. Univ. Press of Kentucky, Lexington.
- Conant, R., and J. T. Collins. 1991. A field guide to reptiles and amphibians. 3rd ed. Houghton Mifflin Co., Boston, MA.
- Cupp, P. V., Jr. 1991. Life history and ecology of the green salamander (*Aneides aeneus*), in Kentucky. J. Tenn. Acad. Sci. 66:171-174.
- Gentry, G. 1955. An annotated check list of the amphibians and reptiles of Tennessee. J. Tenn. Acad. Sci. 30:168-176.
- Gleick, James. 1987. Chaos: making a new science. Penguin Books, New York, NY.
- Gordon, R. E. 1952. A contribution to the history and ecology of the plethodontid salamander *Aneides aeneus* (Cope and Packard). Am. Midl. Nat. 47:666-701.
- Gordon, R. E. 1967. *Aneides aeneus*. Cat. Am. Amphib. Rep.:30.1-30.2.
- Heyer, W. R., A. S. Rand, C. A. Goncalves da Cruz, and O. L. Peixoto. 1988. Decimations, extinctions, and colonizations of frog populations in Southeast Brazil and their evolutionary implications. Biotropica 20:230-235.
- Hutchison, T. C., and M. Havas (eds.). 1980. Effects of acid precipitation on terrestrial ecosystems. Plenum Press, New York, NY.
- Ireland, P. H. 1991. Separate effects of acid-derived anions and cations on growth of larval salamanders of *Ambystoma maculatum*. Copeia 1991:132-137.
- Likens, G. E., R. F. Wright, J. N. Galloway, and T. J. Butler. 1979. Acid rain. Sci. Amer. 241:43-51.
- May, R. M. 1976a. Simple mathematical models with very complicated dynamics. Nature 261:459-467.
- May, R. M. 1976b. Bifurcations and dynamic complexity in simple ecological models. Amer. Natur. 110:573-599.
- Phillips, K. 1990. Where have all the frogs and toads gone? BioScience 40:422-424.
- Pierce, B. A. 1985. Acid tolerance in amphibians. BioScience 35:239-243.
- Redmond, W. H. 1985. A biogeographic study of amphibians in Tennessee. Ph.D. diss., Univ. of Tennessee, Knoxville.
- Shimer, J. A. 1972. Field guide to landforms in the United States. The Macmillan Co., New York, NY.
- Snyder, D. H. 1971. The function of brooding behavior in the plethodontid salamander, *Aneides aeneus*: a field study. Ph.D. diss., Univ. of Notre Dame, Notre Dame, IN.
- Snyder, D. H. 1983. The apparent crash and possible extinction of the green salamander, *Aneides aeneus*, in the Carolinas. (Abstract). ASB Bull. 30:82.
- Williams, K. L., and R. E. Gordon. 1961. Natural dispersal of the salamander *Aneides aeneus*. Copeia 1961:353.
- Woods, J. E. 1968. The ecology and natural history of Mississippi populations of *Aneides aeneus* and associated salamanders. Ph.D. diss., Univ. of Southern Mississippi, Hattiesburg.
- Wyman, R. L., and D. S. Hawksley-Lescault. 1987. Soil acidity affects distribution, behavior, and physiology of the salamander *Plethodon cinereus*. Ecology 68:1819-1827.