

HERPETOLOGICAL HISTORY

Herpetological Review, 2017, 48(3), 576–581.

© 2017 by Society for the Study of Amphibians and Reptiles

Lungless in Highlands: A Brief History of Research and Education on Plethodontid Salamanders at Highlands Biological Station

This paper is a short history of contributions by Highlands Biological Station to our knowledge of the biology of plethodontid salamanders, achieved through research, courses, and conferences. I have interspersed the account of plethodontid studies with essentials of the history of the Station itself, in its mission “to foster education and research focused on the rich natural heritage of the Highlands Plateau, while preserving and celebrating the integrity of the “biological crown of the southern Appalachian Mountains.” In this limited account I cannot include all the individuals, either graduate students or senior investigators, who have studied plethodontids at the Station, but instead will focus on those who have conducted longer-term research at the laboratory. Likewise, I have not provided a full bibliography of scientific papers on plethodontids based on research at Highlands, which would include several hundred citations, but instead provide a short list of major papers and review articles that I hope capture the essence of the types of studies conducted at the Station.

The Highlands Biological Station of Highlands, North Carolina, traces its origin to the establishment of the Highlands Museum Association in 1927, administered through a Board of Trustees of local and summer residents. The association opened a small natural history museum in downtown Highlands in 1928. Shortly thereafter, in 1930, the Trustees invited a group of 15 biologists to a conference to discuss the feasibility of developing a biological research laboratory. Participating in the conference were Clifford Pope of the American Museum of Natural History and his wife and sometime collaborator, Sarah Pope. The conferees were supportive, and the Trustees wasted little time in acting on the recommendations. Land was purchased on Lindenwood Lake, and the Sam T. Weyman Laboratory was constructed in the spring of 1931, opening in July of that year (Fig. 1). Several southeastern universities and colleges joined the association as institutional members that year, and this source of support has continued to the present.

RICHARD C. BRUCE*

Department of Biology, Western Carolina University,
Cullowhee, North Carolina 28723, USA

*Present address: 50 Wagon Trail, Black Mountain,
North Carolina 28711, USA; e-mail: ebruce1563@aol.com

Edwin E. Reinke, an endocrinologist at Vanderbilt University, had been appointed Director of the organization, now renamed the Highlands Museum and Biological Laboratory, in 1930, and he served until 1935. Reinke and his student and colleague, Claude Chadwick, conducted research on the endocrine aspects of the life history of local populations of the newt, *Notophthalmus viridescens*, and contributed several papers in the 1930s and 1940s. Reinke was succeeded as Director by W. C. Coker, a botanist and mycologist from the University of North Carolina, who served until 1944.

Following Coker's resignation, the Laboratory was administered by Acting Director Thelma Howell, who was subsequently appointed Executive Director in 1946. Her succession to the directorship ushered in the era of plethodontid research at the Laboratory. In that summer Clifford Pope, by now at the Field Museum of Natural History in Chicago, returned to Highlands for the summer as Director of the Station's Museum, which provided him sufficient time for field studies of plethodontids. Also in residence was Nelson Hairston, a graduate student at Northwestern University, supervised by the ecologist Orlando Park. Hairston had begun his dissertation research on southern Appalachian plethodontid communities in 1940, but

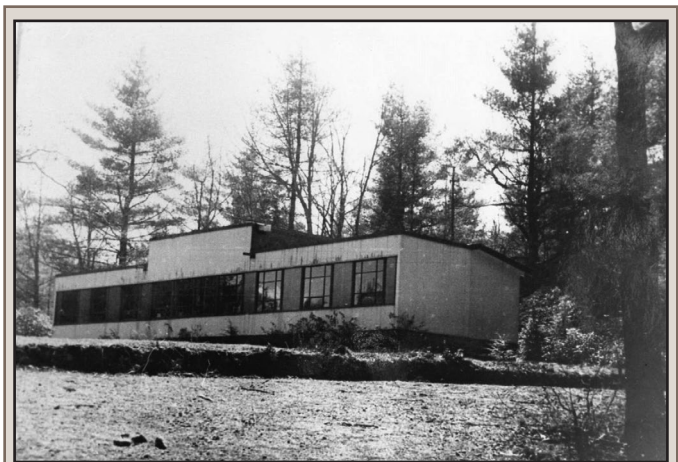


FIG. 1. The Sam T. Weyman laboratory, on Lindenwood Lake, opened in 1931 as the Station's first real research laboratory. It was renovated in 1957, and currently serves as a kitchen and dining hall.

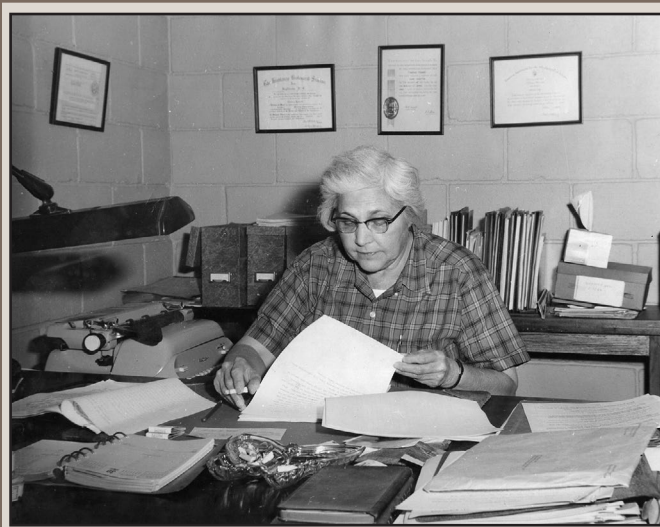


FIG. 2. Thelma "Doc" Howell (1901–1979), Executive Director of the Station, 1946–1972. Doc served on a part-time basis through 1958, holding a concurrent faculty position at Wesleyan College in Macon, Georgia. She was appointed full-time, beginning in 1959, during a period of significant expansion of the Station's programs.

had it interrupted by military service in the South Pacific in World War II. His research at Highlands in 1946 was supported by a scholarship from the University of North Carolina, his undergraduate alma mater. Pope and Hairston collaborated on studies of *Plethodon* and *Desmognathus*, and coauthored several papers appearing in 1947 and 1948. Hairston's landmark dissertation on plethodontid community organization in the southern Blue Ridge was published in *Ecological Monographs* in 1949. Its continuing influence is evident today, e.g., in the 2014 study by Matthew Moskwik in the *Journal of Biogeography* on elevational range expansions of plethodontids of the region.

Although Thelma Howell (known as "Doc" Howell to those of us who studied at the Station during her tenure) was not a herpetologist, she did coauthor several short papers on plethodontids with several students and colleagues (Fig. 2). Doc was a tough-minded, opinionated woman, who didn't mince words. She boldly pursued development of the Station as a research institution, securing major National Science Foundation grants in the 1950s and 1960s for expansion of the physical plant and for field research. With the help and support of Henry Oosting, a distinguished botanist from Duke University, she secured a series of grants for research on the biota of the remote gorges of the southeastern escarpment of the Blue Ridge, then a holding of Duke Power Company's subsidiary, Crescent Land and Timber, and now, in part, Gorges State Park. Several herpetologists participated in the gorge research program, beginning in 1961, including Julian Harrison, Ronald Brandon, and myself. For each of us it represented an entry into plethodontid research at Highlands.

In 1949 the name of the institution, which included the laboratory and museum, had been changed to The Highlands Biological Station. A Board of Managers was established, made up of biologists from the institutional members, to guide the research program. In that summer Robert Gordon, a recent graduate of Emory University, served as Director of the Museum. He and Richard Smith published a short paper on *Aneides aeneus*. Gordon continued this research as a graduate student at the University of Georgia, studying under the ecologist Eugene

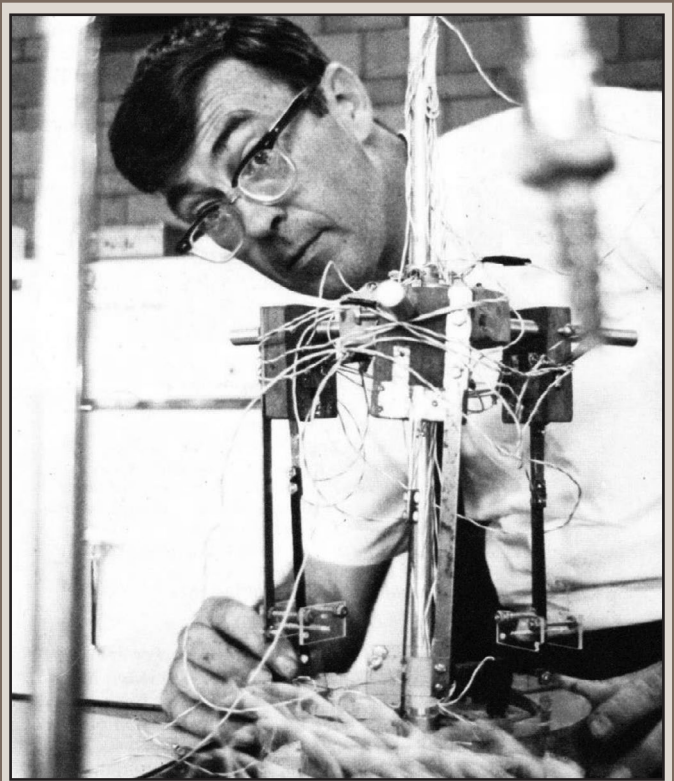


FIG. 3. Robert Gordon, University of Notre Dame, in the laboratory, about 1961.

Odum. Gordon's masters research on *A. aeneus* was published in *American Midland Naturalist* in 1952, and remains an important contribution on the life history and ecology of the species. In the late 1950s and 1960s, as a faculty member at the University of Notre Dame, Gordon and his students, including James MacMahon, Julian Harrison, and David Snyder, returned to the Station during several summers for research on various aspects of plethodontid biology (Fig. 3).

David Wake, then a graduate student at the University of Southern California, conducted dissertation research at the Station in the summer of 1960. He collaborated with Gordon and MacMahon on a study of relative abundance of plethodontids on the Old Yonahlossee Road near Linville, North Carolina, comparing their results to those of E. R. Dunn, who had sampled the same site in 1916. Wake's landmark dissertation on the osteology and evolution of plethodontids was published in 1966. Later, as a faculty member at the University of Chicago and the University of California, Berkeley, Wake returned to the Station during many summers throughout his career to pursue various evolutionary studies of plethodontids. These were conducted with numerous students and colleagues, most notably with Gerhard Roth on the nervous system of plethodontids, as reviewed in Roth and Schmidt (1993). Among Wake's several graduate students who pursued dissertation research at the Station, Sharyn Marks, now at Humboldt State University, conducted important studies of the evolutionary aspects of development, especially skull development, in *Desmognathus*, as well as studies of development in other plethodontids (Wake and Marks 1993; Marks 2000).

During the 1960s and continuing into the 1970s, a significant body of research on plethodontids was carried out by Edmund Brodie, Jr., and his students at Clemson University, on mimicry,

PHOTO BY FRED COYLE



FIG. 4. The Ocoee Salamander, *Desmognathus ocoee*, has been the subject of numerous studies in systematics, ecology, and behavior by many researchers at HBS for more than 50 years.

PHOTO BY FRED COYLE



FIG. 5. The "orange-legged" Red-Legged Salamander, *Plethodon shermani*, of the Nantahala Mountains, the focus of the long-term research on courtship pheromones by Lynne Houck, Steve Arnold, Rick and Pam Feldhoff, and their students and collaborators.

skin toxicity, and defensive behavior in both salamandrids and plethodontids. During the same years, and later, Ronald Brandon, Southern Illinois University, and James Huheey, University of Maryland, collaborated on a number of studies, including mimicry, as well as a major project on rock-face populations of *Desmognathus ocoee* published in *Ecological Monographs* in 1973.

Steve Tilley, as a graduate student at the University of Michigan, initiated field studies at the Station on the life histories and demography of members of the *Desmognathus ochrophaeus* complex in 1967, continuing those studies as a faculty member at Smith College. This phase of Tilley's research culminated in his landmark 1980 paper in *Copeia* on demographics of two rock-face populations of *D. ocoee*. He then turned his attention to *Desmognathus* systematics, and in a number of studies revised our understanding of the relationships of the smaller streamside desmognathines (e.g., Tilley and Mahoney 1995; Tilley et al. 2013).

Don C. Forester, a graduate student at North Carolina State University studying with Bernard Martof, arrived in Highlands in the summer of 1970 to pursue his dissertation research on

parental care in *Desmognathus ocoee*. He returned on many later occasions as a faculty member at Towson University to continue research on various aspects of parental care in this and other species of *Desmognathus* (Masters and Forester 2000).

Thelma Howell retired as Executive Director in 1972, and I succeeded her in June of that year. Toward the end of the summer I received a letter from Nelson Hairston that outlined a long-term experiment he was formulating on competition between members of the *Plethodon jordani* and *P. glutinosus* groups in the Balsam and Great Smoky Mountains. He asked if he could use the Station as a base of operations for the preliminary studies. We, of course, were happy to have Hairston return to Highlands to initiate this project, which he did in the summer of 1973. He outlined the experiment and its possible outcomes in a paper in *Breviora* in December, 1973. The experiment was subsequently conducted, and the principal results were published in *Ecology* and *Evolution* in 1980 and 1981. Hairston followed the *Plethodon* experiments with a manipulative field experiment on *Desmognathus*, conducted at nearby Coweeta Hydrologic Laboratory, the findings published in *American Naturalist* in 1986. Inexplicably, none of these and related publications carried acknowledgments to the Station.

In 1974, Hairston had left the University of Michigan to accept a Kenan Professorship at the University of North Carolina at Chapel Hill. He was later appointed to the Board of Directors of the Station, and subsequently served as its Chair for several years. Thus, the Station had as a leading advocate one of the world's most renowned ecologists, and Hairston's support continued in his retirement years.

Following Hairston's lead, the 1970s and 1980s saw an upsurge of interest in experimental field ecology of plethodontids, by Hairston's students and others, both at Highlands and elsewhere. Hairston's student, Kiisa Nishikawa, examined aggressive behavior experimentally in *Plethodon* in the context of Hairston's findings on competition. Other experimental studies at Highlands include Steven Kleeberger's manipulative experiments on interactions between *Desmognathus quadramaculatus* and *D. monticola*, Christopher Beachy's experiments on interactions among larval plethodontids, and Joseph Bernardo's experimental analysis of resource allocation in *Desmognathus ocoee*. Beachy used experimental cages in the field at Coweeta Hydrologic Laboratory to manipulate numbers of salamanders and examine the effects on survival, growth, and metamorphosis. Bernardo studied essentially the same rock-face populations that Tilley had studied some years before, employing a common-garden design to examine variation in plasticity of life-history traits between high- and low-elevation populations, presenting the results in an important paper in *American Naturalist* in 1998. It is noteworthy that both Hairston (1989) and Bernardo, with William Resetarits (1998), wrote or co-edited, respectively, influential books on experimental ecology.

Lynne Houck, a graduate student at the University of California, Berkeley, then investigating life histories of Neotropical plethodontids under David Wake's supervision, visited the Station briefly in 1975. A few years later, after completing her degree and securing an appointment at the University of Chicago, Lynne returned to Highlands, often with Stevan Arnold, to begin a long series of researches on courtship, mating, and other aspects of the reproductive biology of *Desmognathus* and *Plethodon*, work that involved numerous students and colleagues. One of the latter was Paul Verrell, later at Washington State University. This phase of research by Houck, Arnold, and Verrell was reviewed in

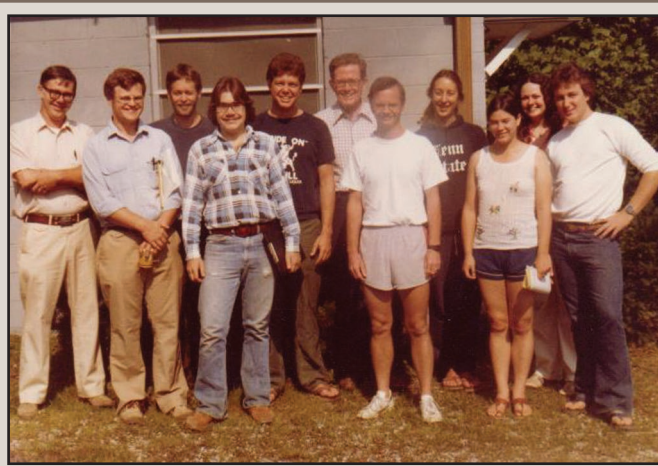


FIG. 6. The first class on the Biology of Plethodontid Salamanders, 1980. Instructors were Richard Bruce, Wayne van Devender, and Nelson Hairston (first, second and sixth from left, respectively).



FIG. 7. The 2006 class on the Biology of Plethodontid Salamanders, shown in the field with instructor Steve Tilley addressing the class.

Houck and Verrell (1993) and Verrell and Mabry (2000). Houck and Arnold later moved to Oregon State University, but have maintained their association with Highlands.

It is noteworthy that from the 1960s onward numerous investigators and their students have used the Station's facilities for studies of behavior, reproductive biology, life history, population ecology, and systematics of *Desmognathus*, mainly focused on *D. ocoee* (Fig. 4). These investigators include Ron Brandon and Jim Huheey, Steve Tilley, Don Forester, Lynne Houck and Steve Arnold, Paul Verrell, and Joe Bernardo. Consequently, our knowledge of the latter species must rank as one of the most complete of any plethodontid.

Lynne Houck and Steve Arnold began a long series of collaborative studies of courtship pheromones with biochemists Richard and Pamela Feldhoff of the University of Louisville in 1991. They were assisted by numerous others, including the Feldhoffs' graduate student, Damien Wilburn, now at the University of Washington, and Sarah Woodley, now at Duquesne University, who had conducted her masters research at the Station earlier, under Houck's supervision, at the University of Chicago. The Houck-Arnold-Feldhoff research carried the investigation of pheromones, primarily in *Plethodon shermani*, to the deep molecular level, as reported in a lengthy series of papers (e.g., Rollmann et al. 1999; Wilburn et al. 2014). The



FIG. 8. A panoply of amphibian/plethodontid specialists, summer 1991. Back row, left to right: Steve Tilley, Paul Verrell, Steve Arnold, Dick Bruce, David Wake, Nelson Hairston, Gordon Ultsch, Richard Wassersug, Jeff Corser. Front row: Elizabeth Jockusch, Sharyn Marks, Sarah Woodley, Neil Shubin.

research continues, as elaborated in recent papers, by Arnold et al. (2017), and Wilburn et al. (2017) (Fig. 5).

In 1973 the Station was approached by Stephen Boyce, Chief Forest Ecologist of the USDA Forest Service, who asked if the Station would be interested in a cooperative research effort to examine the effects of timber harvest, essentially clearcutting, on biotic diversity in southern Appalachian forests. Over the next 25 years a series of cooperative agreements were negotiated with the Forest Service, which supported a broad range of research on the dynamics of vegetation recovery, and on numerous animal taxa in clearcuts of various size, with adjacent mature forests serving as controls. One such study, begun in 1979, and conducted by Andrew Ash of the University of North Carolina at Pembroke, examined the effects of timber harvest on terrestrial plethodontids, mainly *Plethodon metcalfi* and *P. teyahalee*, as reported by Ash in *Conservation Biology* in 1997, and in several other publications.

This project can be considered the first research at Highlands focused explicitly on conservation biology of plethodontids. Later, the USDA Forest Service, through cooperative agreements separate from those of the clearcutting research, funded surveys of the population status of two plethodontid species of concern, *Aneides aeneus* and *Eurycea junaluska*. Given worries about declining amphibian populations globally, much recent research at Highlands since 2000, under the influence of Raymond Semlitsch and his students, as noted below, has been directed at conservation biology of plethodontids.

For its first 50 years, the Biological Station was operated as a private, non-profit institution, under the control of a Board of Trustees, and supported by university and individual memberships, gifts, and grants from various sources. In 1972, negotiations were opened with the General Administration of the newly-reorganized University of North Carolina, i.e., the system of 16 state institutions of higher education, for transfer of the Station to the University. The negotiations were concluded and a transfer document was approved, and by 1976–1977 the Station was a full-fledged interinstitutional center of the University. It was only now that the Station could offer university-level summer courses for credit through one or another of the state universities. The idea was to offer specialized courses on the

PHOTO BY DAVID DENNIS

PHOTO BY LYNNE HOUCK

biota of the southern Appalachians taught by experts in the field, to complement the Station's research program. One of the early courses offered was the Biology of Plethodontid Salamanders, taught in 1980 by Nelson Hairston, Wayne van Devender, and myself, with an enrollment of eight students. The course was later taught by Stephen Tilley, mainly in alternate years from 1983 through 2010, and more recently by Joseph Pechmann and Ken Kozak under the new title Biology of Southern Appalachian Salamanders (Figs. 6, 7). Several other courses on amphibians included plethodontids in their syllabuses, namely Richard Wassersug's course on Larval Amphibian Biology, offered from 1985 to 1997, Ray Semlitsch's Conservation Biology of Amphibians, 2000–2013, and more recently J. J. Apodaca's Conservation Genetics of Salamanders. Thus, over the past 37 years, numerous students have studied amphibian biology at the Station in the summer months, and many have returned to pursue research on plethodontids, as graduate students and postdoctoral investigators. I know of no other field station that has contributed as much to the enhancement of student opportunities for learning of plethodontid salamander biology.

The original Board of Managers was replaced by a Research Committee in 1961 and transformed into the Board of Scientific Advisors in 1976 in the year of the transfer of the Station to the University. The mission of these entities has been to guide the Station's research, and make recommendations on scholarships and grants-in-aid. From its earliest years the Station has provided such support to deserving pre- and post-doctoral researchers, and many students of plethodontid salamanders have received support under this program (Fig. 8). The first Chair of the Board of Scientific Advisors was Joseph Bailey of Duke University, a distinguished herpetologist, who had earlier supervised the present author's graduate studies on *Pseudotriton*, begun at Highlands.

In 1971, an idea was floated that the Station host a conference on plethodontids. A committee was formed, consisting of Steve Tilley, Bob Gordon, Ed Brodie Jr., Doc Howell, and myself. Plans were made, the conference was advertised, the response was positive, and the conference was held in June, 1972, with over 50 participants, including many graduate students as well as the leading senior plethodontid specialists. Subsequent plethodontid conferences, all well attended, were held in 1982, 1992, 1998, and then again in 2016. As I peruse the group photos of the earlier conferences, I recognize many graduate students who subsequently returned to Highlands to conduct research on plethodontids, and whose images appear in group photos of later conferences. The 1992 conference included a special symposium, the proceedings of which were published in *Herpetologica* in the June issue of 1993. The papers presented at the 1998 conference were published as a book, "The Biology of Plethodontid Salamanders," edited by myself, Robert Jaeger, and Lynne Houck, and published by Kluwer/Plenum in 2000. As Andy Ash eloquently stated in the Foreword to this volume, "events such as these are the milestones by which we measure our academic lives." The 2016 conference was designed to celebrate the research on courtship pheromones by Lynne Houck, Steve Arnold, and the Feldhoffs, with the invited papers published in the September 2017 issue of *Herpetologica*.

When I announced my plans to retire as Director of the Station in 1998, there were three exceptionally well-qualified candidates for the position. The search committee offered the directorship to Ray Semlitsch of the University of Missouri. As a herpetologist, I was hoping that Ray would accept the position,

but after a prolonged period of soul-searching he decided to remain at Missouri. Because of his indecision, I remained as Director for another year, when in 1999 Robert Wyatt, a botanist of the University of Georgia, took the position. One of his first actions was to invite Ray Semlitsch to teach a course in amphibian conservation biology at Highlands in 2000. Ray had team-taught the Amphibian Larval Biology course with Richard Wassersug in 1997, and eagerly accepted Wyatt's offer. This led to a productive association of Ray and his students at the Station, shortened by Ray's untimely death in 2015. Several of his students, including William Peterman, Grant Connette, and John Crawford pursued dissertation research on conservation-related aspects of plethodontid biology at Highlands. Given the multiple threats to the welfare of amphibians and other organisms, conservation biology in all its ramifications promises to be an important and necessary future direction of the Station's research and educational programs.

In recent years, through the efforts of James Costa, current Director of the Station, the National Science Foundation has renewed its support of the Station by awarding major grants for substantial renovation of the Station's facilities, including the Coker Laboratory and Biodiversity Laboratory, and ongoing renovations of the Aquatic Laboratory and housing. The modernization of the laboratories should provide unlimited future opportunities for research and education on plethodontid salamanders, in the broader context of the rich biota and diverse ecosystems of the southern Blue Ridge.

Acknowledgments.—Jim Costa, Fred Coyle, Rick Feldhoff, Travis Ryan, Steve Tilley, and Sarah Woodley have been especially helpful to me in preparing this article. I owe a great debt to my late friend, Ralph Sargent, whose book, "Biology in the Blue Ridge: Fifty Years of the Highlands Biological Station 1927–1977," served as an important source for the present article.

LITERATURE CITED

- ARNOLD, S. J., K. M. KIEMNEC-TYBURCZY, AND L. D. HOUCK. 2017. The evolution of courtship behavior in plethodontid salamanders, contrasting patterns of stasis and diversification. *Herpetologica* 73:190–205.
- ASH, A. N. 1997. Disappearance and return of salamanders to clear-cut plots in the southern Blue Ridge Mountains. *Conserv. Biol.* 11:983–989.
- BERNARDO, J. 1994. Experimental analysis of allocation in two divergent, natural salamander populations. *Am. Nat.* 143:14–38.
- GORDON, R. E. 1952. A contribution to the life history and ecology of the plethodontid salamander *Aneides aeneus* (Cope and Packard). *Am. Midl. Nat.* 47:666–701.
- HAIRSTON, N. G. 1949. The local distribution and ecology of the plethodontid salamanders of the southern Appalachians. *Ecol. Monogr.* 19:47–73.
- . 1989. *Ecological Experiments: Purpose, Design, and Execution*. Cambridge University Press, Cambridge, UK. 370 pp.
- HOUCK, L. D., AND P. A. VERRELL. 1993. Studies of courtship behavior in plethodontid salamanders: a review. *Herpetologica* 49:175–184.
- HUHEEY, J. E., AND R. A. BRANDON. 1973. Rock-face populations of the mountain salamander, *Desmognathus ochrophaeus*, in North Carolina. *Ecol. Monogr.* 43:59–77.
- MARKS, S. B. 2000. Skull development in two plethodontid salamanders (genus *Desmognathus*) with different life histories. In R. C. Bruce, R. G. Jaeger, and L. D. Houck (eds.), *The Biology of Plethodontid Salamanders*, pp. 261–276. Kluwer Academic/Plenum Publishers, New York, New York.

- MASTERS, B. S., AND D. C. FORESTER. 2000. Egg recognition cues and maternal behavior in *Desmognathus ocoee*. In R. C. Bruce, R. G. Jaeger, and L. D. Houck (eds.), *The Biology of Plethodontid Salamanders*, pp. 277–286. Kluwer Academic/Plenum Publishers, New York, New York.
- MOSKWIK, M. 2014. Recent elevational range expansions in plethodontid salamanders (Amphibia: Plethodontidae) in the southern Appalachian Mountains. *J. Biogeog.* 41:1957–1966.
- RESETARITS, W. J., JR., AND J. BERNARDO. 1998. *Experimental Ecology: Issues and Perspectives*. Oxford University Press, Oxford, UK. 470 pp.
- ROLLMANN, S. M., L. D. HOUCK, AND R. C. FELDHOFF. 1999. Proteinaceous pheromone affecting female receptivity in a terrestrial salamander. *Science* 285:1907–1909.
- ROTH, G., AND A. SCHMIDT. 1993. The nervous system of plethodontid salamanders: insight into the interplay between genome, organism, behavior, and ecology. *Herpetologica* 49:185–194.
- TILLEY, S. G. 1980. Life histories and comparative demography of two salamander populations. *Copeia* 1980:806–821.
- , J. BERNARDO, L. A. KATZ, L. LOPEZ, J. D. ROLL, R. L. ERIKSEN, J. KRATOVILK, N. K. J. BITTNER, AND K. A. CRANDALL. 2013. Failed species, innominate forms, and the vain search for species limits: cryptic diversity in dusky salamanders (*Desmognathus*) of eastern Tennessee. *Ecol. Evol.* 3:2547–2567.
- , AND M. J. MAHONEY. 1996. Patterns of genetic differentiation in salamanders of the *Desmognathus ochrophaeus* complex (Amphibia: Plethodontidae). *Herpetol. Monogr.* 10:1–42.
- VERRELL, P., AND M. MABRY. 2000. The courtship of plethodontid salamanders: form, function, and phylogeny. In R. C. Bruce, R. G. Jaeger, and L. D. Houck (eds.), *The Biology of Plethodontid Salamanders*, pp. 371–380. Kluwer Academic/Plenum Publishers, New York, New York.
- WAKE, D. B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. *Mem. S. California Acad. Sci.* 4:1–111.
- , AND S. B. MARKS. 1993. Development and evolution of plethodontid salamanders: a review of prior studies and a prospectus for future research. *Herpetologica* 49:194–203.
- WILBURN, D. B., S. J. ARNOLD, L. D. HOUCK, P. W. FELDHOFF, AND R. C. FELDHOFF. 2017. Gene duplication, co-option, structural evolution, and phenotypic tango in the courtship pheromones of plethodontid salamanders. *Herpetologica* 73:206–219.
- , K. E. BOWEN, K. A. DOTY, S. ARUMUGAM, A. N. LANE, P. W. FELDHOFF, AND R. C. FELDHOFF. 2014. Structural insights into the evolution of a sexy protein: novel topology and restricted backbone flexibility in a hypervariable pheromone from the red-legged salamander, *Plethodon shermani*. *PLoS ONE* 9:1–13.