

Introduction to the Special Highlands Conference on Plethodontid Salamander Biology

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ABSTRACT: In August 2016, scientists from the United States and Mexico assembled at Highlands, North Carolina, a temperate-zone hot spot of salamander biodiversity, to participate in the Special Highlands Conference on Plethodontid Salamander Biology. Hosted by the Highlands Biological Station (HBS), the conference celebrated the 90th year of the HBS, and especially the productive collaboration at Highlands of Drs. Lynne Houck, Steve Arnold, and Rick and Pam Feldhoff. The conference showcased the increasing value of plethodontids as research models, exemplified by eight papers in this special issue of *Herpetologica* stemming from invited minireviews presented at the 2016 Special Conference. The papers contribute to the dramatic rise in journal articles that use plethodontids to address diverse questions of broad relevance to modern biology. We hope that this special issue of *Herpetologica* sparks new research on these fascinating salamanders, and we look forward to future conferences on plethodontid salamander biology.

Key words: Amphibian; Biological field station; Urodela

OVER its 90-yr history, the Highlands Biological Station (HBS) has supported a diversity of researchers and research projects that reflects the renowned richness of species and ecological systems of the southern Appalachian Mountains. Perhaps no group of organisms is more emblematic of the region's species richness than plethodontid salamanders (e.g., Fig. 1)—and no research group more emblematic of the rich and productive scientific tradition at HBS than the team headed by Drs. Lynne Houck, Steve Arnold, and Rick and Pam Feldhoff. In celebration of both the retirement of Lynne Houck and Rick Feldhoff and to kick off its 90th year, the HBS hosted a Special Highlands Conference on Plethodontid Salamander Biology—special for the dual occasions it marked, and to distinguish it from the periodic international plethodontid symposia and conferences (which HBS initiated, and hosted, in 1972, 1982, 1992, and 1998). Held from 4 to 7 August 2016, this latest conference was a great success, with more than 100 registrants from across the United States and Mexico, including 29 poster presentations and 37 talks, and several invited minireviews.

The success of the conference and the exponential increase in the number of publications using plethodontid salamanders (Fig. 2) are likely attributable to a diverse combination of features. Plethodontids, with their interesting morphological variation and biogeographic distribution, were at the forefront of early studies on molecular systematics, and a plethora of data are available to test hypotheses about phylogenetic relatedness and the causes and consequences of species diversity. Another interesting feature of plethodontids is that they all possess nasolabial grooves that function in olfaction and pheromonal communication. Hence, plethodontid salamanders are useful for study of signaling systems, and the proteinaceous nature of plethodontid pheromones allowed rapid progress in understanding the biochemical properties and molecular evolution of pheromonal signaling. Finally, plethodontid salamanders are small, abundant, and thrive under laboratory conditions,

which make them well suited for ecological and behavioral studies (Jaeger et al. 2016).

This special issue of *Herpetologica* contains eight papers stemming from the invited minireviews presented at the 2016 Special Conference, following the tradition of publishing presentations from the plethodontid conferences (Houck and Jaeger 1993; Bruce et al. 2000; Bonett and Gifford 2016). Together, the eight papers showcase some of the many contributions of plethodontids to studies of ecology, evolution, behavior, and physiology. The first paper followed in the tradition of Nelson Hairston's classic salamander removal experiments (Hairston 1986) to demonstrate top-down effects of plethodontid salamanders on temperate forest communities (Hickerson et al. 2017). The next two papers deal with the evolution of salamander courtship behavior and courtship pheromones (Arnold et al. 2017; Wilburn et al. 2017). Laboratory observations of salamander courtship behavior, painstakingly collected from many taxa, were summarized, synthesized, and placed in a time-calibrated phylogeny (Arnold et al. 2017). This analysis identified components of the courtship sequence that have been practically frozen in time, static for as long as 170 Myr, likely caused by strong stabilizing selection (Arnold et al. 2017). In contrast, the biochemical and molecular properties of courtship pheromones attest to rapid and incessant diversification, akin to a tango, where male pheromones and female receptors coevolve, constantly moving, around an evolutionary equilibrium (Wilburn et al. 2017).

Three papers in the special issue addressed the evolution of plethodontid diversity. Kozak (2017) examined the causes of species richness over time and space, asking why there are so many plethodontid species at mid-elevation montane habitats, and why the tropics are more species rich compared with temperate zones. Rovito (2017) described patterns of speciation in Mesoamerican plethodontids, testing whether speciation mechanisms varied across latitude within the tropics. Wake (2017) provocatively asked whether the species category has outlived its usefulness, and outlined several challenges and questions for future studies.

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FIG. 1.—A Red-Legged Salamander (*Plethodon shermani*), which is a primary plethodontid model for the collaborative research on pheromonal communication by Lynne Houck, Steve Arnold, Rick Feldhoff, and Pam Feldhoff. This image also served as the logo for the Special Highlands Conference on Plethodontid Salamander Biology. Used with permission from S. Cambridge.

Finally, two papers in this special issue contrasted developmental and physiological processes in plethodontids with those in other taxa. Beachy et al. (2017) described how growth and metamorphosis are decoupled in plethodontids, unlike other salamander families and anurans. Furthermore, they hypothesized that metamorphosis may be less reliant on thyroid hormones compared with other groups, possibly contributing to the pliability of plethodontid life-cycle evolution. Woodley (2017) reviewed studies on stress responses in plethodontid salamanders and concluded that corticosterone, a metabolic hormone, might not mediate many responses to stressors attributable to the remarkably low-energy life style of plethodontids. In addition to the eight papers published in *Herpetologica*, a historical review was presented at the Special Highlands Conference. Readers should see Bruce (2017) for a recounting of the contributions of early plethodontid salamander biologists, many of whom were associated with HBS.

In addition to celebrating plethodontid salamander biology, the conference celebrated the 90th anniversary of HBS as well as the 25-yr collaboration between Drs. Lynne Houck, Steve Arnold, and Rick and Pam Feldhoff. HBS has played a pivotal role in the careers of many of the participants of the conference, either through use of its facilities, enrollment in a summer academic course, or as a recipient of funding. Over the last 35 yr, hundreds of students have enrolled in the courses about plethodontid salamanders, starting with the Biology of Plethodontid Salamanders, taught from 1980 to 2010 and now taught under the new title of the Biology of Southern Appalachian Salamanders. Other courses that included plethodontid salamander biology included Larval Amphibian Biology, Conservation Biology of Amphibians, Landscape Ecology and Conservation of Amphibians, and Conservation Genetics of Salamanders. Many of the students returned to the HBS either as students, postdoctoral fellows, or faculty to conduct research projects, facilitated by generous Grants-in-Aid of research from the Highlands Biological Foundation. The

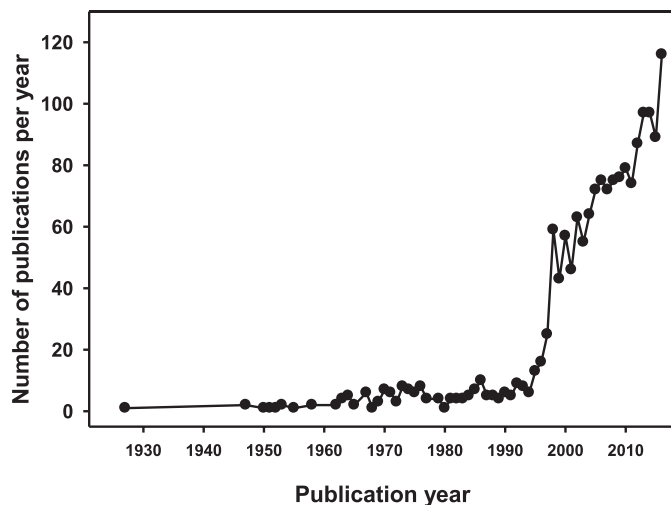


FIG. 2.—A search of Web of Science on 11 January 2017 using the search topic of plethodontid* retrieved 1617 publications from 1927 through 2016. The number of publications with the topic of plethodontid* increased dramatically beginning in the late 1990s and continues to increase, highlighting the continued relevance of the plethodontid salamanders to modern biology.

Grant-in-Aid program has supported research projects for over 60 yr and includes named endowed scholarships, such as the Bruce Family Scholarship for research in herpetology.

The 25-yr collaboration, much of it based at HBS, between Drs. Lynne Houck, Steve Arnold, and Rick and Pam Feldhoff, exemplify the importance of field stations in driving forward scientific progress (Brussard 1982; Klug et al. 2002; Michener et al. 2009; Billick et al. 2013; National Research Council 2014; Tewksbury et al. 2014). Using salamanders collected while staying at HBS, Lynne and her student Nancy Reagan published a seminal paper showing that a crude extract of secretions from the male mental gland increased receptivity to mating in female plethodontid salamanders (Houck and Reagan 1990). Although very exciting, further progress required biochemical expertise. Through a chance meeting on an airplane, Lynne persuaded Rick Feldhoff, a biochemist at the University of Louisville, to investigate the biochemical nature of the secretions, and in 1999, Lynne, Rick, and their student Stephanie Rollman published a groundbreaking paper showing that proteinaceous pheromones increase female receptivity to mating (Rollmann et al. 1999). With understanding of the biochemical basis of the pheromones in hand, the scope of the work rapidly broadened to the evolution of signaling systems at molecular, biochemical, neural, morphological, and behavioral levels, all framed within a rich comparative context. The collaboration grew to include spouses Steve Arnold and Pam Feldhoff. Together, they led and inspired teams of talented students, postdoctoral fellows, and technicians, focusing the work to address important questions of broad biological significance. The work has been funded over the 25-yr collaboration, and a prestigious Integrated Research Challenge in Environmental Biology grant from the National Science Foundation (NSF) brought together additional collaborators including Drs. Ron Gregg, Celeste Wirsig-Weichmann, Fred LaBerge, and Frank Moore. Thus, for 25 yr, a team of plethodontid salamander biologists has

assembled each August at Highlands to exchange ideas, collect material for research, run experiments, and develop lasting friendships.

In 2014, Lynne Houck retired, followed by the retirement of Rick Feldhoff in 2015. Their impressive legacy includes close to 50 papers on plethodontid pheromonal communication, with two more in this special issue (Arnold et al. 2017; Wilburn et al. 2017). The body of work on the evolution of salamander behavior and chemical communication is a classic for understanding the evolution of signaling systems at multiple levels of analysis. Former students and postdocs now populate academic institutions, many with research programs using plethodontid salamanders. Plethodontid research along multiple lines, several inspired by the work of Lynne, Rick, and their students and collaborators, continues unabated at the HBS.

Although the HBS has played an important role in the training and research of many herpetologists over the years, the productivity of plethodontid and other researchers at HBS has in turn benefited the Station. That is because such research productivity has aided efforts to garner further support. Accordingly, since 2005, the Station has received several million dollars from NSF and the State of North Carolina to fund state-of-the-art improvements, including new and improved dormitories, administrative buildings, research and teaching labs, and associated field and laboratory equipment.

As a modern field station in the midst of a temperate-zone hot spot for plethodontid salamander biodiversity, the HBS is a natural choice for regular plethodontid conferences such as the 2016 Special Highlands Conference on Plethodontid Salamander Biology. We look forward to continuing the tradition with future salamander conferences that will celebrate new collaborations and new research directions.

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