



WILLIAM B. HEED  
1926–2007

William Battles Heed (b. June 9, 1926) died September 10, 2007 after a long illness, leaving his spouse of 53 years, Sarah, and three daughters, Ellen, Emily, and Anne. Perhaps best known for his long-term contributions to the ecology, genetics, distribution, and host plant relationships of desert *Drosophila*, Bill Heed was also a consummate field naturalist who came from a long tradition of “knowing” the organisms he worked with. A biography of Heed’s life was recorded as a dedication to the second symposium volume concerning ecology and genetics of *Drosophila* (Fogleman 1990), which included input from him and a complete bibliography, so much of that account will not be repeated. A perspective on Bill’s unique contributions to ecological genetics and evolution early in his career, some relevant references, his pursuit of truth, as well as his insights into science and his colleagues throughout his life, are described here.

Bill Heed was an avid field biologist from a very young age, and he exercised a passion for field ornithology for the rest of life. After graduating from high school, he joined the Navy in 1944 and served in the South Pacific. He obtained his B.S. degree in 1950 from Penn State University, and after some illumination from reading Dobzhansky’s *Genetics and the Origin of Species* (1951), began graduate school at the University of Texas at Austin, becoming John T. Patterson’s last graduate student. Along with Wilson S. Stone, Marshall Wheeler, B. Judd, M. White, and graduate students, a core of soon to be well-known scientists including F. Clayton, T. S. Hsu, J. Hubby, L. E. Mettler, M. Wasserman, M. Seiger, L. Throckmorton, T. Gregg, C. Ward, and visitors such as Th. Dobzhansky and W. Spencer, Heed began his career in the world of *Drosophila*. He immersed himself in the ecology and identification of drosophilids throughout Mexico and Central America on many field trips and developed his expertise in dipteran morphology and species identification under the tutelage of M. Wheeler. A year spent in 1953–1954 in El Salvador describing the ecology of tropical to cloud forest drosophilid communities resulted in his Ph.D. (Heed 1955).

Heed's first academic position was at the University of Pennsylvania in 1956, and he then moved to the University of Arizona in Tucson in 1958 where he spent the rest of his career. Early on, several major expeditions with Marvin Wasserman and Hampton and Meredith Carson from 1956 to the early 1960s signaled the beginnings of long-term collaborations and research into the vast Caribbean drosophilid fauna (Heed and Krishnamurthy 1959; Heed and Russell 1971; Heed et al. 1990; Heed and Grimaldi 1991; Wasserman and Wasserman 1992) and that of Central and South America (Heed et al. 1960; Heed 1963; Heed and O'Grady 2000). One of the most notable hotspots of drosophilid diversity, the Hawaiian Islands, had been studied since the early 1900s (Hardy and Kaneshiro 1981), but it was not until Elmo Hardy and Wilson Stone formed the Hawaiian *Drosophila* project in 1963 (for details, see Spieth 1981), that a concerted effort at understanding the genetics, ecology, systematics, and behaviors of these extremely diverse species began. Heed, along with H. L. Carson, F. Clayton, H. T. Spieth, L. Throckmorton, and H. D. Stalker searched the Hawaiian Islands for endemic drosophilids and began cataloging hundreds of new species. So many undescribed species were found that many were deposited as pinned specimens at the University of Hawaii and labeled as *Drosophila* sp. A, sp. B, sp. C, etc. until there was time for species descriptions to be made (W. B. Heed, pers. comm.). Many of these pinned specimens remain undescribed (Carson 1992), and new descriptions and proposed systematic relationships are still being made (e.g., O'Grady et al. 2003a, b).

Heed realized that host affiliations among some of the major endemic Hawaiian drosophilid clades were very consistent with their proposed phylogenetic groupings, and catalogued hundreds of species' breeding sites by rearing flies out of wild-collected fungi, rotting bark, sap, flowers, and leaves to identify the extent of host specificity (Heed 1968, 1971). His skills as a naturalist and enormous capacity for fieldwork in remote Hawaiian rain forests were complimented by his acumen for identifying the large variety of native Hawaiian plants, as well as being able to discriminate among the huge number of undescribed drosophilids that emerged from these hosts in the laboratory. Heed remained an Associate Entomologist at the University of Hawaii from 1963 to 1970. On a Mexican field trip in the late 1980s, Heed explained his shift away from Hawaiian *Drosophila* in the late 1960s was attributable to the difficulties maintaining relationships with the Hawaiian program so far from Tucson. Heed maintained some ties, but by the mid-1960s, he had already made significant progress in establishing the Sonoran Desert model system of cactophilic *Drosophila* and their hosts. He presented an invited paper (Heed 1989) at Carson's 1986 retirement symposium in Oahu, and corresponded with him until his death in 2004.

Heed's graduate experiences at Texas on field trips throughout the southwest and Mexico and his abiding interest in understanding the role of ecological specificity in drosophilid host plant affiliations formed the basis of the next 40+ years of his research. It became clear that host chemistry was important in driving host specialization (Heed and Kircher 1965; Fogleman and Heed 1989), host preferences in the field and laboratory were strong (Fellows and Heed 1972; Newby and Etges 1998), and the physiology of cactus rots, mediated by microorganisms responsible for tissue fermentation, had to be worked out for a full understanding of the relationships between flies, microbes, and host cacti (Fogleman et al. 1981; Fogleman and Starmer 1985; Starmer et al. 1990). Further, Heed's love for the desert provided ample opportunity for students, associates, and his family to explore the diverse biotic communities in and around the Sonoran and Mojave Deserts on many camping and collecting trips. Heed's expedition planning, later imparted to students and postdocs, always included bountiful food and drink in the most beautiful desert settings that could be found. Heed's talents were also shared as Associate Editor for *Evolution* in 1974, Vice President of the Society for the Study of Evolution in 1976 and the American Society of Naturalists in 1978, program director for systematic and evolutionary biology at NSF in 1976, as well as serving on the advisory board for the *Drosophila* species stock center starting in 1975.

Many of Heed's contributions were possible because of his unique way of motivating colleagues, students (22+ MS and Ph.D.) and postdocs (4). His long association with Henry Kircher, a natural products chemist at the University of Arizona, was essential in describing the unique chemical profiles of giant columnar cacti, later expanded upon by Jim Fogleman. Heed and Kircher both enjoyed the freedom of fieldwork when collecting samples, and Bill always included a vital bit of camping gear, the "Kircher box" containing cooking implements, on many later desert trips. Heed arranged to spend a sabbatical year at UC Davis to work with Herman Phaff in 1972 to begin cataloging and understanding the structure of cactophilic yeast communities. Heed's successful prodding of department colleague A. C. Gibson to take on the systematics of Mexican columnar cacti as a backdrop for understanding *Drosophila* diversification in the desert resulted in a somewhat different career path than the young plant biologist had initially planned. In short, A. C. Gibson successfully worked out the phylogenetic relationships of the many species groups of Mexican columnar cacti after years of intense fieldwork and careful morphological analysis (Gibson and Horak 1978; Gibson 1982). There has yet to be a more comprehensive analysis of these unique plants at either the morphological or molecular levels.

Throughout the 1980s and 1990s, Heed's interest in the Caribbean cactophilic *Drosophila* was rekindled, resulting in three extensive field trips (two by research vessel) initiated by W. T. Starmer (Heed et al. 1990). Heed built long-term international collaborations with researchers in Australia (J. S. F. Barker) and Spain (A. Fontdevila and A. Ruiz). His willingness to share unpublished data resulted in a number of synthetic papers and reviews (Etges and Heed 1992; Etges et al. 1999). He remained active as a collaborator on NSF grants

and helped to expand the study of phylogenetic (Durando et al. 2000) and host plant relationships in cactophilic *Drosophila* to all of Mexico, and Central and South America, particularly in the large (100+ species) *Drosophila repleta* group.

For years, Heed had dedicated himself to the study of species differences and patterns of reproductive isolation between newly described species, many of which were difficult or impossible to rear under laboratory conditions. A testament to his scientific standing was the respect of his peers: four species were named for him in the genera *Laccodrosophila*, *Scaptomyza*, *Drosophila*, and *Cladochaeta*. His fascination with nature was infectious, and he continued to generously share his knowledge and expertise with colleagues. Heed continued to go on desert collecting trips until his health prevented him from traveling. He kept his laboratory open until well after retirement in 1992 and continued to train some of us in the Zen of *Drosophila* species descriptions and the biology of poorly known species.

Heed remained indefatigable through the last few years. He participated in the *Drosophila* species Stock Center workshops passing down some of what he knew to younger workers. He continued working on a meta-analysis of *Drosophila* faunal diversity throughout the arid lands of North America based on his knowledge of species distributions throughout the southwestern United States and Mexico. He and his collaborators collected much of these data. Some results were published (Oliveira et al. 2005), but the comprehensive analyses of faunal resemblance remain unfinished. Until his last days, he continued to try to finish another species description in collaboration with colleagues based on collections he made in the 1970s and 1980s (Heed and Castrezana, unpubl.ms. 2007). He never seemed to lose his fascination with understanding how nature has been shaped by biological diversification.

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