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Research

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Papers From a Workshop on Mosquito Ecology and Evolution Inspired by the Career of L. Philip Lounibos

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Mosquitoes attract attention and the interest of scientists because of their immense importance as vectors and pests. Emergence and re-emergence of vector-borne diseases such as dengue (Thomas et al. 2016), West Nile encephalitis (Rizzoli et al. 2015), Zika (Weaver et al. 2016), chikungunya (Weaver 2014), and most disturbingly yellow fever (Grobbelaar et al. 2016, Paules and Fauci 2017, http://www.who.int/news-room/fact-sheets/detail/yellow-fever) have added urgency to understanding the biology of mosquitoes as vectors. This important aspect of the biology of mosquitoes is one emphasis of *The Journal of Medical Entomology*. However, mosquitoes also are fascinating organisms from the perspective of basic investigations of ecology and evolutionary biology (e.g., Kneitel and Chase 2004, Ellis et al. 2006, Griswold and Lounibos 2006, Leisnham et al. 2009, Urbanski et al. 2012, Brown et al. 2014, Resetarits and Silberbush 2016, Zeller and Koella 2017, McIntire and Juliano 2018). They are useful and in many cases highly tractable study systems for many basic questions of animal biology that have proved to be important for improved understanding of mosquitoes as vectors, and our efforts to limit the harm that they can cause.

The recent retirement of Distinguished Professor L. Philip Lounibos of the Florida Medical Entomology Laboratory, University of Florida, provided mosquito biologists with the opportunity to bring together multiple conceptual aspects of ecology and evolutionary biology of mosquitoes in a workshop. Our workshop commemorates his long and successful career of research on the basic ecology and evolutionary biology of mosquitoes (https://scholar.google.com/citations?hl=en&user=spFINlIAAAAJ&view_op=list_works&sortby=pubdate). That career led 23 of his former students, post-doctoral researchers, and collaborators to present a series of talks related to the research themes Phil pursued and inspired (Fig. 1) (DOI 10.6084/m9.figshare.6848993). Most of the talks dealt with the basic aspects of mosquito biology, rather than mosquito control, but there is little doubt that the wealth of knowledge generated by these research directions has improved our understanding of mosquito distribution and abundance, adaptive evolution, pathogen transmission, and invasion biology, all of which are important for making sound decisions about public health interventions. During the discussion at the workshop, Graham White noted the multiple advantages that accrue to researchers following Phil's example of a mosquito ecology career: contributing practical effort to limit the harm caused by disease vectors and producing basic research that interests academic ecologists and evolutionary biologists. A sample of the workshop's talks appear in this special issue.

Phil's academic career included both a traditional pedigree in biology and unconventional choices that provided him with a unique perspective on many of the fundamental issues in vector biology. He grew up in northern California with a childhood fascination of insects, especially moths. His interest in insects followed him to Notre Dame, where, as an undergraduate, he worked in the laboratory of the famed culicidologist George Craig. While at Notre Dame in the Craig lab he interacted with other undergrads who later established research careers using insects as model systems, such As Jim Truman (University of Washington & HHMI); Fred Nijhout (Duke University), Jeff Powell (Yale University), and Bill Conner (Wake Forest University). From Notre Dame, Phil took a position as a doctoral student in the laboratory of the pioneer of insect endocrinology, Carroll Williams, at Harvard University. An interesting aside to Phil's Harvard education was his insistence, and indeed fight, to count Spanish as a foreign language for the doctoral program. At the time, PhDs in the biological sciences were expected to demonstrate competency in two of the three major languages of science: French, Russian, or German. Phil rightly recognized the practical importance of Spanish and was able to pass the standard exam in this language in the place of one of the better-recognized languages of science. This would prove prescient, as Phil's later career included substantial projects in Latin America. While his doctoral dissertation harkened back to his childhood fascination with Lepidoptera (cocoon spinning behaviors of silkworms, Lounibos 1974), he maintained his undergraduate interest in mosquitoes. Indeed, he established some important collaborations in mosquito biology at Harvard, especially with a post-doctoral fellow and office mate, William (Bill) Bradshaw.

Phil and Bill would go on to collaborate on several projects on the ecology of mosquitoes, particularly concerning diapause strategies and the evolution of dormancy in the North American pitcher plant mosquito, an interest Bill continued throughout his career (Bradshaw and Lounibos 1972, 1977; Bradshaw et al. 2003).

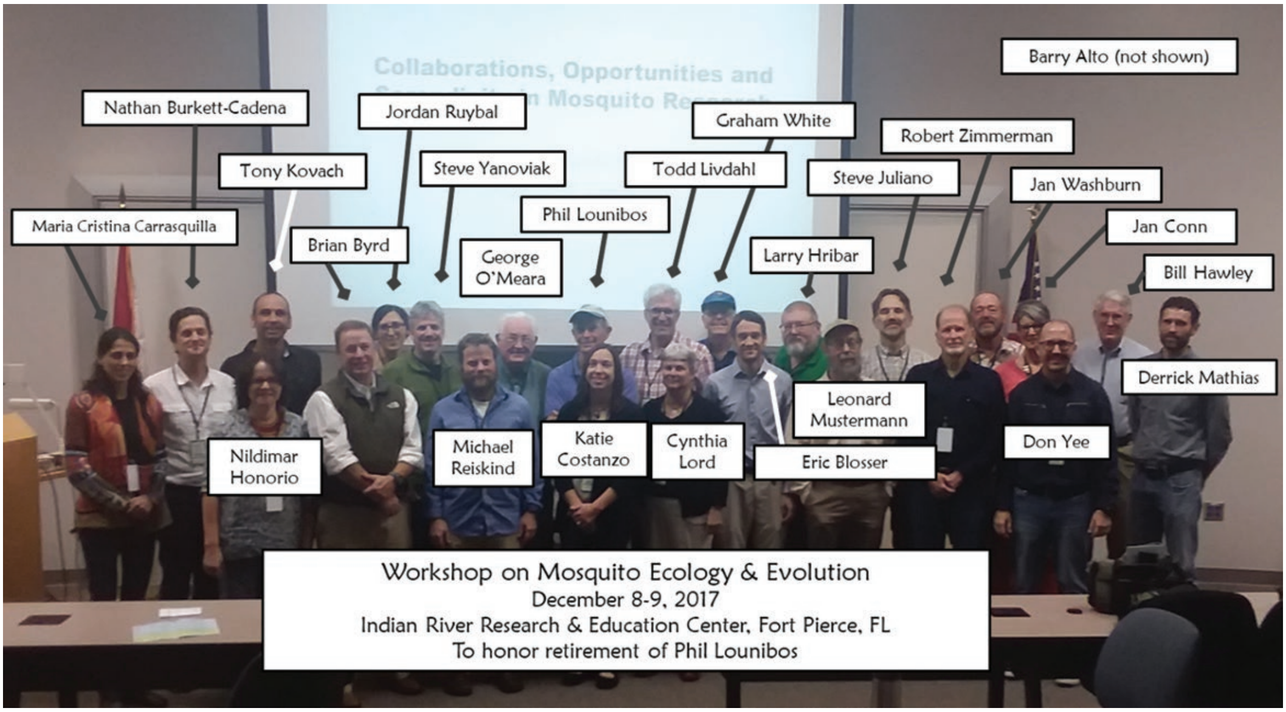

Fig. 1. Workshop presenters.

After Phil completed his dissertation, he decamped from Harvard for Kenya, where he held a position as a research scientist at the International Center for Insect Physiology and Ecology and Head of ICIPEs Coastal Research Station and Mosquito Biology Unit in Mombasa. His research in Kenya focused on mosquitoes in phytotelmata, especially treeholes, and field tests of genetic methods for control of *Aedes aegypti* (L.) (Diptera: Culicidae) in coastal villages (Petersen et al. 1977, Lounibos 2004). It was during this period that he discovered the first and only Afrotropical anopheline known to occupy a phytotelm habitat (Lounibos 1979); subsequently this species was described as *Anopheles lounibosi* Gillies and Coetzee 1987 (Diptera: Culicidae).

After his stint in Africa, Phil took a job at the Florida Medical Entomology Laboratory (FMEL) in the pursuit of field research on mosquitoes, which was, at the time of his hire, administered by the Florida Department of Health and Rehabilitative Services. Here he was also reunited with one of his colleagues from Notre Dame, George O'Meara. Within a few years FMEL would be integrated with the University of Florida in the Department of Entomology and Nematology.

Phil would spend the next four decades at the FMEL, with projects ranging from studying the fascinating behavior and ecology of *Mansonia* (e.g., Lounibos and Linley 1987, Lounibos and DeWald 1989), the biosystematics of South American malaria vectors (e.g., Lounibos et al. 1998, Lounibos and Conn 2000), and the communities of mosquitoes in treeholes and other phytotelmata (e.g., Lounibos 1983, Lounibos et al. 1993). He also edited, along with Jorge Rey and Howard Frank, one of the true classics in mosquito ecology, *Ecology of Mosquitoes: Proceedings of a Workshop* (Lounibos et al. 1985). He mentored multiple doctoral students and post-doctoral scholars over his time at the FMEL, many of whom have continued in academia. Other mentees have pursued careers in mosquito control, government service, and public health. His diverse career at the FMEL was generously supported by grants and fellowships from the U.S. National Institutes of Health, U.S. National Science Foundation, and State contracts, which for the past two decades have focused on the ecology of invasive mosquitoes, primarily *Aedes albopictus* (Skuse).

Invasive mosquitoes are central to understanding vector-borne disease as many species transmit emerging disease agents (Lounibos 2002). Understanding the processes operating on invasive mosquitoes provides vital knowledge that can lead to better surveillance for diseases (Lounibos 2002), better forecasts of future threats (e.g., Lounibos and Kramer 2016), and better interventions to limit disease (e.g., Bonsall et al. 2010). Examples from Phil's work illustrate how information about the basic biology of mosquito vectors can be of practical value. Invasion of North America by *Ae. albopictus* began with colonization of the port of Houston, TX, in the late 1980s (Hawley 1988). The spread of *Ae. albopictus* to the North and East was rapid, so that by the late 1990s it was widespread and common in the southeast, and still spreading (Moore and Mitchell 1997). The spread was associated with a decline, sometimes to local extinction, of *Ae. aegypti*, a previous invader from Africa of long tenure in North America (Lounibos 2002). The ecological and evolutionary mechanisms behind this successful invasion and apparent displacement of *Ae. aegypti* were the subject of numerous hypotheses, including interspecific competition among larvae, apparent competition via host-specific parasites, and mating interference (reviewed by Lounibos 2002), and the possibility that declines of *Ae. aegypti* were independent of the arrival of *Ae. albopictus* (Hawley 1988). Work by Phil and his collaborators firmly established that the combination of *Ae. albopictus* having superior competitive performance as larvae (e.g., Braks et al. 2004, Camara et al. 2016) and an advantage in mating interference (Bargielowski and Lounibos 2014, 2016; Lounibos and Juliano 2018) has driven this invasion success and impact on *Ae. aegypti*. The detailed work has documented context-dependent variation in these interactions on local and global scales (Leisnham et al. 2009; Bargielowski et al. 2013, 2015a,b; Bargielowski and Lounibos 2014, 2016; Honório et al. 2017). The result is a richer understanding of which species is likely to dominate in different areas and where coexistence is likely (Lounibos and Juliano 2018). Further work by Phil and his collaborators documented the evolution of diapause in invading *Ae. albopictus* (Lounibos et al. 2003, 2011). That work shed light on the continuing spread of this species into climatic regions that had been predicted to be unsuitable based on the characteristics of the species in its native range, and inspired wider investigations of the evolution of diapause in this species (Urbanski et al. 2012). Understanding the determinants of distribution and abundance of these two important vectors affects planning for control efforts directed specifically against one or the other species (e.g., Bonsall et al. 2010), and the complex possibilities for virus transmission where coexistence is possible (Lord 2010). Further work by Phil and his students showed the potential for ecological interactions among larvae to influence vector competence of adults and ultimately virus transmission (e.g., Alto et al. 2005, 2008; Alto and Lounibos 2013). It seems clear that Phil's research has yielded both a valuable understanding of vector ecology and evolution in a changing and complex world and inspired other researchers to pursue similar questions in different systems and locations (e.g., Urbanski et al. 2012).

The papers in this special section provide a sample of the kinds of basic questions pursued or inspired by Phil. Bargielowski et al. (2018) evolution of resistance to mating interference and its role in the invasion of *Ae. albopictus* and the reductions of *Ae. aegypti* associated with that invasion. This work documents the potential for adaptive evolution of both species when they encounter each other. Carrasquilla et al. (2018) present new data on the effects of body size on spermathecal filling in *Ae. albopictus*. Rogers and Yee (2018) test for context dependent effects of detritus type as modulators of intraspecific competitive interactions of larval *Ae. albopictus* and *Ae. aegypti* that could affect local distribution and abundance. Juliano et al. (2018) report results of a field experiment testing whether *Toxorhynchites* predation is a barrier to invasion by *Ae. japonicus*. Beyond invasions and *Ae. albopictus*, Fitzgerald and Livdahl (2018) investigate habitat partitioning of *Aedes triseriatus* and *Aedes hendersoni* in sympatry and allopatry, and present data consistent with competitive character displacement (Germain et al. 2018) in oviposition choices. Zimler and Alto (2018) investigate the virus–vector interaction of Florida *Aedes* and Zika virus.

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