TALES OF PARASITOIDS AND VIRUSES

By Nancy Beckage Professor of Entomology & Cell Biology and Neuroscience

Parasitoids, polydnaviruses, and hosts: Who’s in control? My laboratory focuses its efforts in deciphering how parasites and pathogens interact with their host on the physiological, biochemical, and molecular levels. Parasitoids kill their host, and in the process alter their host’s immune system, hormones, metabolism, and behavior. The parasitoid *Cotesia congregata* feeds only on host hemolymph and physiologically manipulates its host through induction of changes, which suppress the host’s immune system and induce host developmental arrest in the larval stage. The wasp injects a polydnavirus (PDV) into host tobacco hornworm larvae during parasitization, and the virus elicits host immunosuppression so the parasitoids can develop without becoming encapsulated by host hemocytes. Jean-Michel Drezen (now with the CNRS in Tours, France) demonstrated that PDV sequences are integrated in the wasp’s genomic DNA as a provirus. Thus, the PDVs are genetic symbionts of the wasp, which act as a vector to disseminate the viral particles to host larvae during oviposition. The polydnavirus acts in concert with the parasitoids to manipulate the physiology of the host for the parasitoid’s benefit.

Why the tobacco hornworm? *Manduca sexta* is a particularly valuable insect for studying physiological changes invoked by parasitism because it’s immune system and endocrine physiology have been well-characterized. Comparisons with parasitized insects can therefore be readily made. Also, probes such as antibodies are available to monitor levels of hemolymph proteins, neuropeptides, and other molecules in this insect. The large size of the host larvae allows us to purify hemolymph proteins, collect endocrine and nervous tissues for biochemical analysis, implant parasitoids into nonparasitized larvae, and perform other physiological manipulations, which would be simply unfeasible using smaller insects. Results of our studies using parasitized tobacco hornworms have proven valid for many other relationships of lepidopteran hosts with wasp endoparasitoids.

Host immune disruption: Insect AIDS and baculoviruses: Graduate student Steve Harwood (now at Invitrogen in Carlsbad, CA) characterized an early viral transcript of the *C. congregata* PDV and purified and sequenced this virally encoded protein from the hemolymph of newly parasitized caterpillars. With Steve McElfresh (from Jocelyn Millar’s laboratory), who field-collected several sphingid species for us, we examined the hemolymph proteins of several permissive and non-permissive hosts that encapsulated *C. congregata* eggs. This “early protein 1” was expressed in permissive hosts, but was absent in the nonpermissive species, suggesting its presence is correlated with successful suppression of host immunity. Graduate student Mark Lavine (now at the University of Wisconsin in the lab of Mike Strand) observed that the hemocytes of newly parasitized tobacco hornworms underwent apoptosis and could not encapsulate foreign targets; the PDV caused this effect. Graduate student Nghiem Le has examined expression of another PDV viral transcript, the *Cotesia rubecula* CrV1 gene product, which Otto Schmidt’s lab has determined disrupts hemocytes in hosts of *C. rubecula*. Working in collaboration with Sarjeet Gill of UCR, we determined that the temporal expression of the *C. congregata* CrV1 homolog occurs for several days following oviposition. Our next goal is to clarify whether the CrV1 homolog expressed in *M. sexta* inhibits the host immune system from encapsulating parasitoid eggs. Injection of *C. congregata* PDV dramatically increases susceptibility of *M. sexta* to the *Autographa californica* M nuclear polyhedrosis virus (AcMNPV), as found in a recent collaborative study we did with Loy Volkman and Jan Washburn at the University of California-Berkeley. Frances Tan of our lab provided critical support by dissecting several thousand wasps for PDV purification, and Eric Haas-Stapleton of the Volkman laboratory assisted by tracking the fate of the injected larvae. Larvae that are parasitized or injected with PDV prior to inoculation with AcMNPV die much sooner compared to larvae infected with AcMNPV only. The cellular immune system of the larva is compromised by the PDV, and so the AcMNPV infection spreads rapidly throughout the hemocoel. Our next goal is to identify which PDV genes products enhance baculovirus pathogenicity and use those genes to bioengineer more virulent baculovirus insecticides with a faster speed-of-kill and broader host range than the viruses currently in use.
Parasitoids as host endocrine disruptors: Our collaboration with Dale Gelman at the USDA/ARS Insect Biocontrol Laboratory in Beltsville, MD has yielded fascinating insights into the role of ecdysteroid as a signaling molecule in parasitized larvae. Darcy Reed, who is now in Tim Paine’s and Jocelyn Millar’s lab, and Frances Tan provided assistance. A peak in the host’s ecdysteroid titer occurs the day before the wasps emerge from the host. In vitro culture of the parasitoids demonstrated that the wasps secrete ecdysteroids into the their host’s hemolymph. We have a collaboration with Tracey Webb and Sonny Ramaswamy at Kansas State to assay the juvenile hormone titre of parasitized larvae, and determine if the parasitoids similarly secrete JH.

Hormonally active insect growth regulators disrupt emergence of the wasps. Undergrad Regina Foreman analyzed the inhibitory effects of application of methoprene, a juvenile hormone analogue, to host larvae on emergence of the wasps. We are now analyzing the hemolymph of methoprene-treated hosts to see if the normal pre-emergence ecdysteroid peak is suppressed, thereby preventing wasp emergence. Frances Tan, with undergrads Anil Date and Jerusalem Tesfai, assessed effects of administration of ecysdone and its agonists on development of parasitized larvae. These compounds trigger molting of the host and interfere with wasp emergence.

We’ve also found that parasitism also inhibits release of neuropeptides from the neurosecretory system when the host lingers with emerged wasps without molting, as shown by Dusan Zitnan. Tim Kingan, now at UCR, showed that the processing of FLRF-amides in the midgut endocrine cells of the host is inhibited. Thus, a shutdown in neuropeptide processing and release appears to be induced during development arrest.

Yet another insult: parasitic castration: Darcy Reed observed that even though parasitized tobacco hornworms are destined to die before they reproduce, their testes are prevented from proliferating in the last instar and undergo cell death and atrophy. Many parasites cause castration of their host, but the underlying physiological mechanisms responsible for shutting down host reproduction remain obscure in most cases. Nutrients that would otherwise fuel host reproduction are thus made available to the growing parasites.

Parasitoid manipulation of host behavior and growth: Host anorexia is induced by infection in a wide range of animal species. Parasitized larvae cease feeding before their parasitoids emerge, and this is adaptive for the parasitoids which would be consumed by a feeding host. Hundreds of species of parasitized insects show a similar behavior when their parasitoids emerge. Shelley Adamo, now at Dalhousie University, demonstrated that the normal reflexive behaviors of the host are retained while feeding and spontaneous locomotion stop. Shelley found that a peak in hemolymph octopamine occurs when the wasps emerge, and hypothesized that this biogenic amine may suppress feeding in larvae with emergent wasps. Carol Miles and Ron Booker of Cornell University have recently tested this hypothesis, using neural recordings from the frontal ganglion which regulates food intake in M. sexta. They found that octopamine, and a component of hemolymph from hosts with emerging wasps (presumably octopamine), inhibits firing of the frontal ganglion. Thus, a rise in octopamine levels may be the critical factor that causes host anorexia.

What is even more amazing is that the host’s growth during the last instar is very precisely modulated by the wasps. Graduate student Marianne Alleyne, currently finishing her Ph.D at the University of Illinois, found that hosts with many parasitoids attained a higher final weight than hosts with fewer wasps. The possibility that the parasitoids secrete metabolic hormones to influence host growth has yet to be addressed.

ALUMNUS FEATURE

Our featured alumnus for this issue is Professor Michael E. Irwin. He is the Schlinger Arthropod Biodiversity and Systematics Research Scholar in the Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana–Champaign. Irwin joined the faculty and staff of the University of Illinois and Illinois Natural History Survey in 1974 after working for three years as the curator of insects at the Natal Museum, Pietermaritzburg, South Africa. He holds a joint appointment with the Department of Entomology, University of Illinois, and with the Centers for Economic Entomology and Biodiversity, Illinois Natural History Survey.

Irwin received a BS in Entomology from the University of California at Davis in 1963 and a PhD in Systematic Entomology in 1971 from the University of California at Riverside. His doctoral research at UC Riverside was supported by a National Defense Education Act Fellowship and focused on the systematics and ecology of therevids (Diptera: Therevidae), a rarely encountered family of flies. Although his studies took him to many parts of Western North America, his primary field site was the P. L. Boyd Deep Canyon Desert Research Center near Palm Desert, where he and his major professor, Evert I. Schlinger, sampled and studied arthropods for more than five years. One notable experience that occurred during Irwin’s graduate tenure at UCR was a 14 month research stay in Chile as a member of the University of California–University of Chile Collaborative Program, sponsored by the Ford Foundation. While in Chile, he worked at first under Martin Barnes and then Schlinger on his dissertation research. Another experience was a half-year expedition to East Africa under the leadership of Edward S. Ross of the California Academy of Sciences. After joining the University of Illinois' International Soybean Program (INTSOY) in the autumn of 1974, his efforts focused on the international aspects of integrated pest management (IPM) of soybeans. He assisted lesser developed countries in developing and deploying IPM programs for soybean and other crops, partly through harmonizing research and extension efforts and convincing national teams to determine and employ action thresholds for management decisions.

Irwin's research focus was predicated on an amazing paucity of knowledge concerning the management of epidemics of plant viruses transmitted by insects. In particular, he spent a large portion of his career investigating ways to reduce, delay, and retard epidemics caused by potyviruses transmitted nonpersistently by aphids. These viruses are the most widespread, most devastating, and perhaps the most difficult group of viruses to manage, worldwide. His seminal research on Soybean Mosaic Virus epidemiology led him to conclude that a very fruitful management avenue to pursue was the manipulation of environmental factors, taking into account changes in behavioral
response, in particular flight and settling responses, of aphids that vector this virus. This led him to a 15-year study of movement of aphids, both within-field and over longer distances (migratory flight). In 1996, the "Award for Outstanding Achievement in Biometeorology" was bestowed on him by the American Meteorological Society for this research effort.

Irwin maintains a presence in international IPM. He is the sole external member of the Integrated Pest Management Collaborative Research Support Program's (IPM CRSP) Technical Committee, the Deputy Executive Director of the Consortium for International Crop Protection (CICP), and was Convener of Session 2, Agricultural Entomology, for the XXI International Congress of Entomology, Iguacu Falls, Brazil, August 2000.

In 1994, the National Science Foundation initiated a new program entitled Partnerships for Enhancing Expertise in Taxonomy (PEET). PEET provided Irwin an avenue for returning to his first research love, the systematics and ecology of therevids. He was successful in securing a 5-year grant in 1995 and a renewal in 2000. His project, "Towards a world monograph of the Therevidae," supplemented by Schlinger Foundation resources, has successfully advanced a phylogenetic framework on which to hang this monographic pursuit. He and his systematics team have made considerable headway towards this end (see http://www.nhfs.uiuc.edu/cee/therevid/). In 1999 Irwin was elected an Honorary Fellow of the California Academy of Sciences, based in part on the merits of this systematic undertaking. Perhaps the trait that most characterizes Irwin's research career is a team approach. He has a remarkable ability to assemble and lead multidisciplinary teams. Each of his major research thrusts (plant virus epidemiology, aphid movement, and therevid systematics) has been distinguished by a broad, transdisciplinary approach, and each has benefited enormously from it.

On a personal note, Irwin plays squash and enjoys collecting insects. At the end of his current NSF/PEET grant in September 2005, he plans to continue his systematic pursuit of therevids in retirement. He and his wife Bonnie plan a move to the Southwest where the winters are warmer and the out-of-doors more inviting. Irwin can be contacted at m-irwin2@uiuc.edu.

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**IN MEMORIAM**

Professor Emeritus Lauren D. "Andy" Anderson passed away August 25, 2000 at the age of 91. Dr. Anderson joined the Citrus Experiment Station faculty in 1948 as an Associate Entomologist. He retired from the UCR Entomology Department as an Emeritus Professor in July 1976. Dr. Anderson’s work at the Citrus Experiment Station in Riverside laid much of the groundwork for the kind of research characteristic of UCR today. His projects included controlling insect pests on vegetable crops, insecticide toxicity, honeybees, and aquatic midge control. The course he developed in identification of immature insects and his enthusiasm for his subject stimulated his students and his colleagues in UCR's Entomology Department to collect and contribute to his growing collection of immature insects. This led to UCR's appointment of the first Curator of the Entomology Collection in the early 1960s and in 1993, with the construction of the Entomology Research Museum, to a unified collection under one roof. Because of Professor Anderson's tireless and groundbreaking efforts, UCR's immature insect collection is one of the largest and best in the western United States. His legacy continues through the Lauren D. and Mildred D. Anderson Endowed Graduate Assistantship in Immature Insects which ensures that the finest graduate students can and will come to UCR to study in this critical field.

Professor Emeritus George P. Georghiou passed away November 6, 2000, at his home in Riverside at the age of 74. Dr. Georghiou joined the UCR Department of Entomology as a junior specialist in 1958, after he received B.S. and M.S. degrees from Cornell University. In 1960, he received his doctorate from Berkeley and became a lecturer at UCR. He was named an associate professor in 1967 and received a promotion to full professor two years later. Before his retirement from full-time teaching and research in 1995, he served as head of the Division of Toxicology and Physiology for eight years (1975 to 1983) and as chairman of the Entomology Department for a year (1983-1984).

Dr. Georghiou focused his research on the genetic, physiological, and behavioral mechanisms in insects that result in insecticide resistance. Mosquitoes and houseflies were the primary objects of his research, both as model systems for the evolution of resistance in insects and because of the serious threats to human health they represented. He co-authored 141 scholarly articles and four books; developed widely used field tests for the monitoring and management of resistance; maintained computerized databanks about documented cases of insecticide resistance; and was an early investigator into the efficacy of biopesticides, including the bacteria *Bacillus thuringiensis* (Bt). His laboratory was designated as a Reference Center for Pesticide Resistance by the U.N. Food and Agriculture Organization, and he received funding from the World Health Organization, the U.S.-France Collaborative Science Program, and the U.S. Army Medical Research Program, as well as industry and state agricultural agencies. He also served on several national and international scientific advisory boards.

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**AWARDS AND HONORS**

John Klotz has been awarded the 2000 Distinguished Service Award for Outstanding Research (Specialist), presented on behalf of the Academic Assembly Council Program Committee of UC Cooperative Extension. Greg Walker received the Pacific Branch ESA Teaching Award and Nancy Hinkle was awarded the Pacific Branch ESA “Distinguished Achievement Award in Extension” at this year’s Pacific Branch meeting in Costa Mesa. Nancy Beckage and Tom Miller are UCR representatives on the Editorial Board of a new electronic journal, the Journal of Insect Science, to be produced entirely online by the University of Arizona library. Dave Hawks will have a feature article “Jewel Scarabs” and the cover in an upcoming issue of National Geographic. This article highlights research by Dave, and Ron Cave from Honduras, on the ecology of these rather spectacular beetles. Brian Federici has been appointed again as a member of the U.S. Environmental Protection Agency’s Scientific Advisory Panel on Plant-Pesticides. Kristen Michel and Jeb Owen received awards for the best graduate student presentations at the Department Student Seminar day, September 2000. Kristen for Ph.D. and Jeb for M.S.
The Entomology Department is making great strides as it moves into the new century. We recruited for two new positions in 1999-2000 (we will run profiles of our new faculty in future copies of The Buzz), and we will recruit for two more in 2000-01. The program areas that will be bolstered by the new additions include population genetics, behavior, pathogen transmission, and integrated pest management.

In addition to new positions, the new Insectary and Quarantine facility is scheduled to open in early 2001. As you can read in John Heraty’s article in this issue, this new building will greatly increase our capability to conduct biological control projects as well as other research requiring containment facilities.

In an earlier issue of The Buzz, we described the construction of our new Entomology laboratory and office building. As of this week, the construction crews have finished pouring the concrete for the second story walls of the west wing and the third story floor plate for the south wing of the building. The mass and scale of the spaces are now becoming clear as the flat architectural drawings we have poured over for so long are now being transformed to three dimensions.

We have planned several special spaces within the building. Hundreds of elementary school children crowd our hallways each year looking at the small number of display cases we maintain. While we encourage their fascination with insects, the display spaces are limited and the narrow halls outside the research labs and offices reverberate with their enthusiasm. To solve the dilemma in the new building, we will have expanded display areas on each floor off the large glass atrium between the wings. In addition to the educational displays, we have planned additional spaces to display the awards and feature the accomplishments of our students and faculty. A separate area will be set aside to highlight outside sponsors of departmental research and teaching programs. Finally, we intend to provide spaces to prominently display insect art. The lobby atrium, the courtyard garden, and the outside walls provide a number of opportunities for displays.

We need your help. We are looking for suggestions from you as to what type of art you feel would be aesthetically enduring, convey the excitement, fascination, and beauty of insects to the members of the public as they come into the building, and highlight the importance or impact of our science. We have been thinking of some type of sculptural element, and suggestions have included a large standing metal sculpture, a dynamic mobile, a glass sculpture or glass tiles, or sculptural insects mounted on the outside walls. We are also looking for names of artists that create this type of work (at a reasonable cost). Please send me your suggestions (timothy.paine@ucr.edu). If the artists have internet sites, please let me know that as well. Our goal is to commission a piece that celebrates the accomplishments of all the individuals who have been part of the department and inspire those who will come in the future. Your experiences are an important part of meeting that goal, and I encourage you to contribute your suggestions.

Department of Entomology
University of California
Riverside, CA 92521

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