Journal of Insect Behavior, Vol. 17, No. 5, September 2004 (© 2004)

In Praise of a Good Colleague: Ronald John Prokopy

Daniel R. Papaj[1]

Ronald J. Prokopy passed away unexpectedly on May 14, 2004, at the age of 68. He was a devoted student of insect behavior, a long-standing contributor to the Journal of Insect Behavior and, for many in the field, an exceptional colleague.

R.J. Prokopy

Ronald John Prokopy was born on September 28, 1935, in Danbury, Connecticut. Ron, as he was known to everyone, grew up on a farm. He earned bachelor and doctoral degrees at Cornell University. Ron studied migratory behavior in alfalfa weevils for his dissertation, but his life's research concerned the behavior of insects that exploited tree fruit as hosts, most notably tephritid flies. The contributions that Ron Prokopy made to our science are reflected in an impressive list of publications, unbroken success in grantsmanship, a solid lineage of successful students and postdocs, the successful application of knowledge about insect behavior to pest management, and the high regard in which he and his work are held. Beyond these achievements, the following "key words" and phrases apply to Ron:

[1]Department of Ecology & Evolutionary Biology, University of Arizona, Tucson, Arizona 85721.

0892-7553/04/0900-0569/0

energy, enthusiasm, stubbornness, a passion for insects, generosity, loyalty, competitiveness, quirkiness, idealism, "can do" spirit, intensity.

Ron began studying tephritid flies while working at the Connecticut Agricultural Experiment Station from 1964 to 1968. After a brief stint at the Swiss Federal Research Station in Wädenswil, Switzerland, he joined the University of Texas in 1969 as a research associate, studying fly behavior alongside noted evolutionary biologist Guy Bush. The pair established what would become a long-standing collaboration on the biology of the apple maggot fly, *Rhagoletis pomonella*, and a lifelong friendship. In 1974, Ron established the Prokopy Bio-Experimental Farm in Bailey's Harbor, Wisconsin. There, in a brief time, he conducted seminal studies of *Rhagoletis* behavior and ecology, while living out of a small trailer and raising his newly-born son Josh, with his wife, Linda. In 1975, Ron joined the faculty of the Department of Entomology at the University of Massachusetts in Amherst, where he worked on the behavior of tephritid flies, plum curculio, and other tree fruit insects for the remainder of his life.

THE WORK

Ron's work in the 1960s and 1970s on *Rhagoletis* behavior is archetypal for the study of mechanism in insect behavior, especially with regard to its field component (cf. Prokopy, 1968). The combination of simple but elegant laboratory and field assays that characterized his work, with its seamless integration of naturalistic observation and experimental manipulation, stands as a model that many of us still emulate, and encourage our students to emulate. In that early work is reflected a recurring theme in Ron's approach to understanding insects, namely a holistic perspective in which every aspect of the insect's biology—oviposition, mating and feeding, chemical cues and visual cues, larval and adult stages, experience and physiological state—was subject to scrutiny by Ron and his students, postdocs, and collaborators. The questions asked were straightforward, as were the experimental designs employed. Yet taken together, the studies are a tour de force in terms of the separate studies connecting one to another to tell a complete story of an insect's behavior in nature. Ron's approach, as embodied not only in his work, but that of a robust lineage of students, postdocs, and academic descendants helped to make tephritid flies a model system in the study of insect behavior.

Ron's research projects began inevitably in the context of the insect's natural history. Through long hours of observation of flies in apple and hawthorn trees, for example, he characterized the mating system of the apple maggot fly, reporting a seasonal shift from a foliage-based

system of diffuse male aggregation to a fruit defense system (Prokopy *et al.*, 1971), describing courtship (Prokopy and Bush, 1973), and providing evidence of male and female sex pheromones. From those basic observations, later work followed, which documented last-male sperm precedence in that species (Opp and Prokopy, 1990) and multiple mating. Ron also demonstrated the existence of an oviposition-deterrent host-marking pheromone in tephritid flies (Prokopy, 1972). Frustrated in decades-long collaborative efforts to identify the chemical constituents of the pheromone (tephritid host-marking pheromones being notoriously unstable and difficult to characterize), he and students studied instead the dynamics of its effects on oviposition behavior (Roitberg and Prokopy, 1981, 1983; Averill and Prokopy, 1988) and its role in diminishing larval competition (Averill and Prokopy, 1987). While we still do not know the chemical structure(s) of host-marking pheromone in apple maggot fly, it is fair to say that the description of the function and dynamics of pheromone responses made an original and far-reaching contribution to the field.

Ron devoted much attention to host selection behavior. His work emphasized the role of visual and olfactory cues. Ron was ahead of his time in using spectrophotometry to aid in the construction of visually mimicking models of fruit and leaves (Prokopy *et al.*, 1983). Work led by Martin Aluja showed that fruit odor arrested female apple maggot flies in apple trees, but did not otherwise facilitate localization of individual fruit within trees under field conditions (Aluja and Prokopy, 1992). Ron and students also explored the interaction of olfactory and visual cues in host selection (Aluja and Prokopy, 1993; Green *et al.*, 1994).

The host selection research in general reflects the influence of one of Ron's lifelong inspirations, John S. Kennedy, who viewed host selection behavior as a catenary process, a series of phases linked inextricably one to the other. With apple maggot fly in particular, Ron and colleagues systematically explored each of the relevant phases, from tree finding to fruit finding to fruit acceptance. In terms of the details in which these phases are described, perhaps only the foraging behavior of honey bees is as well characterized in insects. The degree to which Ron emulated J. S. Kennedy in his approaches is embodied in a passage from Ron's Entomological Society of America Founders' Memorial Award lecture which was presented as a tribute to Kennedy:

> …[Kennedy] was able to formulate astute hypotheses addressing factors underlying behavioral patterns and was able to create ingenious (often extremely simple) experimental approaches and apparatus to evaluate these hypotheses. He became legendary for the incisiveness with which he teased apart the nature of orientation responses of insects to visual and odor stimuli and for coming to grips, at the most subtle level of detail, with how orientation responses were affected by the physiological state of the insect and the state of the environment. (Prokopy, 1999)

The passage is an apt description of Ron himself, though Ron differed from Kennedy in trading depth in the study of orientation mechanisms for breadth in coverage of other areas such as host acceptance, mating, and feeding behavior.

Some of these areas proved to be more difficult than others, for example, the subject of fruit fly feeding biology. The topic was challenging with respect to adults because adults are highly opportunistic with respect to food source and often feed off the host tree, and challenging with respect to larvae because of the complex microbial community characteristic of the fruit rot on which larvae feed. The biology of feeding gave itself up grudgingly, but progress made by Ron and colleagues nonetheless set the stage for more effective strategies for food-based control of tephritid flies (Hendrichs *et al.*, 1993; Lauzon *et al.*, 2000). Here, as in much of his work, Ron's signal contribution was the joining of two spheres of endeavor: pursuit of basic knowledge and the application of such knowledge to pest suppression. Ron blurred the line between basic and applied research, to such an extent that the distinction holds little meaning in consideration of his work.

Ron was long fascinated by the dynamics of oviposition behavior, as influenced by physiological state (with J. Duan, B. Roitberg, and A. Averill), experience (with S. Cooley and D. Papaj), and social factors (with J. Duan, R. Dukas, C. Nufio, D. Papaj, J. Piñero, and J. Rull). In his studies of the role of learning and physiological state in egg-laying behavior, Ron was influenced again by Kennedy, and also by Vincent Dethier, who had given these topics prominence in his own work on flies.

With respect to learning, Ron once again brought a natural history context to a subject long restricted to the laboratory domain. He provided some of the earliest evidence for the role of experience in shaping host preference in an insect, doing so at a time when the evolution of host preference was a hot topic in evolutionary biology and when sources of variation in preference, such as genetics and learning, were being studied intensively (Prokopy *et al.*, 1982; Papaj and Prokopy, 1988). Ron asked straightforward but original questions, for instance, do host races or biotypes differ in how host experience affected oviposition preference (they do; Prokopy *et al.* 1986; Prokopy and Papaj, 1988), and is male territorial behavior influenced by prior experience with one or another host fruit species (it is; Prokopy *et al.*, 1989)?

Topics of keen basic research interest to Ron in recent years were local enhancement of fruit alightment and social facilitation of oviposition behavior (Prokopy and Duan, 1998; Piñero and Prokopy, 2004), processes in which flies were induced by the presence of flies on fruit, first, to land on those fruit and, second, to lay eggs. This work, like much of his work, has

a strong comparative bent, indicating that social effects are of broad significance in tephritid flies. However, social effects have also proven inconsistent in their expression (Dukas *et al.*, 2001), suggesting that they are conditional upon as-yet-unknown variables. The most recent studies (Piñero and Prokopy, 2004; C. Nufio, D. Papaj, and R. Prokopy, in preparation) suggest that the density at which flies are held prior to testing may be a factor.

As regards the dynamical nature of oviposition behavior, and in his behavioral studies generally, Ron's special contribution was to bring these ideas to bear upon the theory and practice of Integrated Pest Management (IPM), an ecologically sensitive approach to managing pests. One of the early leaders in IPM in this country, Ron invented the "sticky red sphere trap" widely used for monitoring apple maggot fly populations, or for direct control of this pest without using harsh chemicals. The characteristics of the trap, as well as the manner in which it was deployed in an orchard, was a direct result of Ron's basic research studies of the fly's behavior. These studies showed males and females to be maximally attracted to a sphere of slightly larger-than-apple size that contrasted strongly against background. The trap, now marketed as a red plastic ball treated with a sticky coating, markedly reduced the frequency and intensity of pesticide spraying. A second-generation trap, impregnated with a biocide and incorporating odor attractants, was under development by Ron and colleagues at the time of his death, and stands to promote use and effectiveness at the commercial scale. Ron's research-based recommendations for trap placement and density (with F. Drummond and E. Groden), as shaped by information about effects of experience and physiological state, were perhaps as important to the trap's success as the components of the trap itself.

A similar connection between basic behavioral research and IPM was made for another fruit pest, plum curculio (with L. Phelan, S. Butkewich, and T. Lemsky). Ron's contributions to IPM did not stop at the level of behavioral research and development either. He interacted intensively with fruit growers from the outset of his career in Massachusetts, regularly attending growers' meetings and tirelessly advocating IPM strategies. On his farm in Conway, Massachusetts, which he shared with Linda and sons Josh and Max, Ron maintained a small orchard, growing Liberty, Freedom, and other disease-resistant varieties of apples. Ron raised his apples according to IPM principles that he himself had a strong hand in establishing. He sold his apples as IPM, low spray produce in local stores. Ron's success in "practicing what he preached" greatly enhanced his credibility among apple growers and contributed further to reduced pesticide use in New England.

THE COLLEAGUE

Ron Prokopy was a prolific author, with over 450 publications to his credit. Two papers appeared in the journal *Science*, and one in *Nature*. Fourteen publications appeared in the *Journal of Insect Behavior*, spanning the journal's maiden volume to the present issue. Ron received a Guggenheim fellowship and a Fulbright research award, and sat on the editorial boards of the journals *Protection Ecology* and *Chemical Ecology*. Along with Guy Bush, he was "the" person to contact for review of manuscripts on fruit fly biology, and rarely shirked his duty in this regard.

Coincident with the staggering list of publications was an equally impressive record of continuous research funding over his 30 years as a faculty member, with over 5.25 million dollars in competitive grant awards, despite no award greater than $350K and most in the $50K–100K range. As anyone who worked with Ron knew, he was generous to a fault in distributing funds for travel, supplies, and stipends. However, his generosity taxed supply, and demanded frugality in turn. Ron's respect for the value of a research dollar was nowhere more evident than in the field vehicles used in orchard work. Over the years, the fleet included a bright yellow Ford Torino with uncertain brakes, several immense station wagons with deteriorating floors, and a Korean War surplus MASH ambulance. Wrote University of Massachusetts colleague Dan Cooley (pers. comm.), "Some days, I think Ron's powerful will to understand the orchard ecosystem was the only thing that kept those cars going." In Ron's view, money was far better spent on people, on assistants, students, technicians, and postdocs, than on late-model vehicles or, for that matter, most other forms of technology.

Ron was notorious for eschewing technological advances ranging from the growth chamber to the video camera. To say that Ron was not "hi-tech" in his approach to the study of behavior is an understatement; he was essentially "no-tech," and proud of it. He reveled, for example, in the reliability of his spartanly equipped fly rearing and observation room, which lacked any sophisticated temperature or humidity controls that might break down. To the end of his life, he remained more comfortable writing notes on recycled scraps of paper or using the telephone, rather than composing e-mail. One might send Ron an e-mail and a week or more later, receive a reply that seemed to have been written or transcribed by an assistant. Needless to say, the cost and short time to obsolescence of personal computers and software distressed Ron.

As these anecdotes suggest, Ron was a colorful character, appreciated almost as much for his eccentricities as for his science. Perhaps nothing exemplified these eccentricities more than a modest shoulder bag that Ron carried with him everywhere he went. Of Guatemalan origin, the bag generally contained scraps of paper on which he would write scarcely legible

notes, one or two freshly prepared manuscripts, and usually, some form of healthy food such as neatly wrapped, thinly sliced carrots from his garden, or a small bag of granola. When the bag's strap broke, Ron fashioned a new one from white cotton clothesline. When the clothesline subsequently bit uncomfortably into his shoulder, he fitted the strap with a pad cut from a piece of sponge. His distinctive appearance harmonized with an effervescent, disarming personality, and a genuine gift for conversation.

Ron was known for his discipline and strict adherence to routine, perhaps a product in part of time spent in the Army. In his daily life, Ron adopted an "ironman" regimen well before the term came into its current usage. He was an early riser and engaged in vigorous exercise, jogging daily, swimming in his orchard pond, cross-country skiing in winter to his bus stop and back, chopping wood, and scrupulously maintaining his garden and orchard. Whether at meetings, or on visits to orchards, or during research trips, colleagues were hard pressed to keep up with him.

Ron was a creature of habit in sometimes quirky, occasionally exasperating ways, whether it was pancakes each Sunday (religiously), two vegetables at dinner (always), flossing after meals (including in restaurants and the occasional student exam!), and a daily nap wherever he might be and whenever the moment struck him. Ron was very particular about what he ate, to the point of eccentricity; when he traveled abroad, he might bring an entire suitcase filled with granola, vitamins, and other items not easily obtained on site.

Other, less curious habits contributed mightily to the vitality of Ron's research. He devoted the entire month of January each year to reading in the library, catching up on the latest material on old themes, and initiating reading on new ones. He made annual research trips to Hawaii over most of the last 20 years, studying (with T. Wong and R. Vargas) a variety of tropical fly species, including the Mediterranean fruit fly and Oriental fruit fly.

Ron was addicted to meetings as well, particularly international ones. From his vantage point, science had no political boundaries. He was advisor to graduate students from Canada, Mexico, and China, and made innumerable trips throughout the world, establishing collaborations and, invariably, friendships with colleagues in Europe, Asia, Australia, and Central and South America (E. Böller, S. Finch, E. Städler, R. Drew, B. Fletcher, B. Katsoyannos, and A. Malavasi, among many).

THE FRUIT FLY

The fruit fly accomplishes quite a lot in a relatively brief lifetime. So too, did Ron Prokopy. One of the enigmas concerning Ron is how he could write so many papers, gather so much grant money, attend so many

meetings, conduct so much extension work, give so many seminars, review so many manuscripts, supervise so many students, technicians, and postdocs, contribute so much in service to his department, yet still have the time, not to mention the energy, to maintain a small orchard and sell its produce, take his boys to Fenway for baseball games, go to New York for the opera or to Tanglewood for jazz, attend rallies for liberal causes, sing in the local chorus, hike with Linda, and, more recently, dote on his granddaughter Annabel. Ron loved sports too, having been a member of the ice hockey team at Cornell. He was an avid runner, swimmer, golfer, cross country skier, skater, and fly fisherman. How did he fit it all in? Somehow, he did.

Ron professed more than once his desire to be reincarnated as a fruit fly. Some would say that Ron in a past life must already have been one, so keen were his insights about their behavior. Without doubt, the most impressive attribute that Ron brought to bear upon the study of tephritid flies, plum curculio, and other tree fruit pests was his intuition about their behavior. Ron truly had a "feeling for the organism," as regards these insects. Intuition is a powerful, if perhaps underappreciated, driving force in science, and we stand to advance our knowledge about insect behavior more slowly than we might have, owing to Ron's premature passing.

On Saturday, May 22, 2004, Ron's ashes were distributed among the apple trees of his orchard in Conway, Massachussetts, by his wife Linda and his sons Josh and Max. Family, friends, and colleagues were in attendance.

ACKNOWLEDGMENTS

The author thanks Guy Bush, Laura Carsten, Tom Green, Beth Jakob, Cesar Nufio, Adam Porter, Bernie Roitberg, and Emilie Snell-Rood for comments on a previous draft.

REFERENCES

Aluja, M., and Prokopy, R. J. (1992). Host search behavior of *Rhagoletis pomonella* flies: Intertree movement patterns in response to wind-bourne fruit volatiles under field conditions. *Physiol. Entomol.* **17:** 1–8.

Aluja, M., and Prokopy, R. J. (1993). Host odor and visual stimulus interaction during intratree host finding behavior of *Rhagoletis pomonella* flies. *J. Chem. Ecol.* **19:** 2671–2696.

Averill, A. L., and Prokopy, R. J. (1987). Intraspecific competition in the tephritid fruit fly, *Rhagoletis pomonella. Ecology* **68:** 878–886.

Averill, A. L., and Prokopy, R. J. (1988). Factors influencing release of oviposition-deterring pheromone by *Rhagoletis pomonella* flies. *J. Chem. Ecol.* **14:** 95–111.

Dukas, R., Prokopy, R. J., Papaj, D. R., and Duan, J. J. (2001). Egg laying behavior of Mediterranean fruit flies (Diptera: Tephritidae): Is social facilitation important? *Flo. Entomol.* **84:** 665–671.

Green, T. A., Prokopy, R. J., and Hosmer, D. W. (1994). Distance of response to host tree models by female apple maggot flies: Interaction of visual and olfactory stimuli. *J. Chem. Ecol.* **20:** 2393–2413.

Hendrichs, J., Fletcher, B. S., and Prokopy, R. J. (1993). Feeding behavior of *Rhagoletis pomonella* flies: Effect of initial food quantity and quality on food foraging, handling costs and bubbling. *J. Insect. Behav.* **6:** 43–64.

Lauzon, C. R., Sjogren, R. E., and Prokopy, R. J. (2000). Enzymatic capabilities of bacteria associated with apple maggot flies: A postulated role in attractancy. *J. Chem. Ecol.* **26:** 953–967.

Opp, S. B., and Prokopy, R. J. (1990). Factors influencing estimates of sperm competition in the apple maggot fly, *Rhagoletis pomonella*. *Ann. Entomol. Soc. Am.* **83:** 521–526.

Papaj, D. R., and Prokopy, R. J. (1988). The effect of prior experience on components of habitat preference in the apple maggot fly, *Rhagoletis pomonella*. *Oecologia* **76:** 538–543.

Piñero, J. C., and Prokopy, R. J. (2004). Local enhancement of alighting in the melon fly: Effect of olfactory, visual and acoustical stimuli. *J. Insect. Behav*. **17:** 493–510.

Prokopy, R. J. (1968). Visual responses of apple maggot flies, *Rhagoletis pomonella* (Diptera: Tephritidae): Orchard studies. *Entomol. Exp. Appl.* **11:** 403–422.

Prokopy, R. J. (1972). Evidence for a pheromone deterring repeated oviposition in apple maggot flies. *Environ. Entomol.* **1:** 326–332.

Prokopy, R. J. (1999). The power of observation: A tribute to John S. Kennedy. *Am. Entomol.* **45:** 161–172.

Prokopy, R. J., Averill, A. L., Cooley, S. S., Roitberg, C. A., and Kallet, C. (1982). Associative learning in egglaying site selection by apple maggot flies. *Science* **218:** 76–77.

Prokopy, R. J., Bennett, E. W., and Bush, G. L. (1971). Mating behavior in *Rhagoletis pomonella.* I. Site of assembly. *Can. Entomol.* **103:** 1405–1409.

Prokopy, R. J., and Bush, G. L. (1973). Mating behavior in *Rhagoletis pomonella*. IV. Courtship. *Can. Entomol.* **195:** 973–991.

Prokopy, R. J., Collier, R. H., and Finch, S. (1983). Leaf color: A character used by cabbage root flies to distinguish among host plants. *Science* **218:** 76–77.

Prokopy, R. J., Cooley, S. S., Kallet, C., and Papaj, D. (1986). On the nature of learning in oviposition site acceptance by apple maggot flies. *Anim. Behav.* **34:** 98–107.

Prokopy, R. J., Cooley, S. S., and Opp, S. B. (1989). Prior experience influences fruit residence of male apple maggot flies. *J. Insect. Behav.* **2:** 39–48.

Prokopy, R. J., and Duan, J. J. (1998). Socially facilitated egglaying behavior in Mediterranean fruit flies. *Behav. Ecol. Sociobiol.* **42:** 117–122.

Prokopy, R. J., and Papaj, D. R. (1988). Learning of apple fruit biotypes by apple maggot flies. *J. Insect. Behav.* **1:** 67–74.

Roitberg, B. D., and Prokopy, R. J. (1981). Experience required for pheromone recognition by the apple maggot fly. *Nature* **292:** 540–541.

Roitberg, B. D., and Prokopy, R. J. (1983). Influence of host fruit deprivation on apple maggot fly response to oviposition deterring pheromone. *Physiol. Entomol.* **8:** 69–72.