H O W A R D E. E V A N S 1919-2002

A Biographical Memoir by MARY JANE WEST-EBERHARD

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HOWARD E. EVANS

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BY MARY JANE WEST-EBERHARD

Howard Ensign Evans, one of the twentieth century's leading entomologists and insect natural historians, was born in Hartford, Connecticut, the son of Archie James Evans and Adella Marian Ensign. He was also, in his spare time, a talented writer of popular books and articles on natural history and conservation.

Howard Evans's love of nature began on the Evans family farm near East Hartford, Connecticut, a 60-acre tobacco farm that was purchased, with the help of financing from his maternal grandfather, Howard Ensign, when his parents were married. Howard's mother was his father's second wife. She had been teaching school after having studied education at a normal (state teachers') school, and Howard was her only child, though he had a stepbrother and three stepsisters by his father's first marriage.

In his childhood Howard Evans was strictly an applied entomologist. Here is what he wrote about that stage in his life.

I suspect that when most people dig into the recesses of their minds for their earliest childhood memories they come up with scenes of kittens, puppies, or hamsters. My earliest memories are of tobacco hornworms, and how delightfully they pop and ooze between bare toes. Picture a tobacco farm in the Connecticut Valley, with kids walking up and down the rows looking for big, green caterpillars and executing them by the most primitive of control measures (Evans, 1985, p. 145).

As a youth, Howard helped to found the Hockanum Nature Club, a museum in a woodshed with collections of pressed leaves, wildflowers, birds' eggs, and insects. The name of the club came from the local American Indian name for the region of the Evans farm in East Hartford. Howard Evans undoubtedly had something to do with choosing the name, for later he often used indigenous words as names for new species of insects discovered during his travels, for example, naming the Australian sand wasp Bembix mianga, a fly-catching species, after the aboriginal word (mianga) for "fly," and B. uloola, a bright orange species, after the aboriginal word, uloola, for "sun" (Evans and Matthews, 1973). His "first wealth (several dollars!)" came when he sold to a neighborhood hobbyist some of the moths that were attracted to the lights of the family fruit stand (Evans, 1968a, p. 25).

Life on the farm was ended not by tobacco hornworms but by a series of hailstorms and a drop in the tobacco market that eventually drove Howard's father to other crops and eventually to bankruptcy during the Great Depression of the 1930s. But his rural background was a lasting influence and inspiration. Even as an undergraduate Howard wrote, in a classroom essay on "Experiences With Insects,"

I think the modern mind tends to debunk, or at least to minimize, the values and advantages of being country bred. . . . But I am sure that the appreciation of country life is merely going under a cloud, and will emerge again when the people once more take to the country rather than swarming in the cities like flies on rotten fruit. . . . Although my family moved away from the farm into the suburbs a few years ago, my absence from the country has tended to accentuate rather than suppress my affinity for the things of nature. . . . My hobbies then were not the ordinary ones, such as stamp or coin collecting, but consisted of recording the living things I saw,

especially the birds, and, best of all, collecting insects. . . . I was an odd but happy figure in those days, roaming the countryside with a net in one hand and a pair of binoculars in the other. . . . I first became really interested in insects when I began to notice the attractiveness of certain moths which swarmed around the street lights. . . . The idea of making a net and of mounting what I caught in boxes of cotton covered with glass was adopted from a friend engaged in the same diversion. I soon became fanatic about the business, and, much to my parents' disgust, spent hour after hour chasing "bugs" over field and stream.

Howard credited his father with his "workaholic tendencies," and said that he was encouraged in his interest in natural history by his mother, who taught him the names of many birds, insects, and stars. Even so, when he went to the University of Connecticut in 1936 he started out as an English major. He switched to biology after his first course in entomology, taught by J. A. Manter, described by Howard as "a very unusual teacher," who "in his quiet way . . . introduced me to the world of professional entomology" (Evans, 1968a, p. 25). After writing an undergraduate thesis on insects reared from the downed trees and branches of the 1938 hurricane, he graduated magna cum laude in 1940.

The intention to major in English probably reflected his lifelong passion for writing. His first book was a volume of poetry titled *The Song I Sing* (Evans, 1951), a compilation of poems previously published in the Hartford newspapers. During spare moments while later in the army he wrote a novel that he later destroyed. Throughout his active life as a scientist he wrote popular books, not all of them related to entomology. The best known of his 16 books, *Life on a Little-Known Planet* (Evans, 1968a), was translated from English into French, German, and Japanese, and was reprinted many times during the more than 30 years that it has remained in print. Unlike some popularizers of science, Evans did not lose respect in science as a result of his popular writing, because his scientific output—a lifetime total of 265 scientific publications, including a number of books and monographs—was undiminished by his avocation as a writer for the general public. It was as if he led two highly productive lives in perfect harmony with each other.

Immediately after college graduation Howard worked at the Connecticut Agricultural Experiment Station in New Haven, and then went to Cornell, where he completed a master's thesis on spider wasps (Pompilidae). Then, in December of 1941, while he and his mother listened to the New York Philharmonic on the radio, indulging a love of classical music acquired while in college, he learned of the attack on Pearl Harbor. Howard asked his draft board to move his name to the top of the list. He spent four years in the army. Because he already had a master's degree in entomology, he was assigned to be a medical laboratory technician in a hospital in Newfoundland, where he discovered that a mysterious ailment of servicemen was being caused by the parasite Giardia. Probably as a result of that discovery he was promoted to second lieutenant upon return to the United States. He spent the rest of the war at a base hospital in North Carolina working as a parasitologist on stool samples from servicemen returning from the Philippines. In one of his books (Evans, 1985, p. 125), he said of this experience that "in a grim and odorous way, it was rather fun." Following this interlude of service in the army he was able to return to graduate studies at Cornell without financial problems, thanks to the GI bill. At Cornell, with J. Chester Bradley and V. S. L. Pate as cochairmen of his doctoral committee, he finished a doctoral thesis on the systematics of the tribe Pompilini (Hymenoptera, Pompilidae), and then joined the faculty of Kansas State University in Manhattan, Kansas, as assistant professor of entomology.

At Kansas State he taught courses on general entomology, immature insects, and morphology and curated the insect collection (from an unpublished "History of the Department of Entomology, KSU," by Herbert Knutson, deposited in the department; courtesy of John Reese). There he spent three productive years (1949-1952) studying the behavior and systematics of sand wasps, along with his graduate students Carl Yoshimoto and C. S. Lin. During this time he expanded his general interest in animal ethology with the encouragement of a fellow faculty member, A. M. Guhl, a well-known student of social dominance in chickens, and read works by Lorenz, Tinbergen, Thorpe, and others. During this period, he also took a summer field trip to Mexico with the late Paul D. Hurd, Jr., of the University of California.

Howard Evans and Mary Alice Dietrich were married in 1954, soon after Mary Alice had finished her Ph.D. in science education at Cornell and not long after Howard had returned to work there as assistant professor of entomology in 1952. They had three children, Barbara (Galloway), Dorothy (Tuthill), and Tim. Mary Alice was the daughter of the Cornell entomologist Henry Dietrich, who had "warned his daughters to stay away from entomologists, who were likely to be impecunious and little appreciated by society." "Fortunately," Howard wrote, "Mary Alice failed to take his advice" (Evans, 1985, p. 217). Howard declared in his autobiographical notes that "few persons have been lucky enough to enter a partnership with someone so congenial and supportive." He considered his marriage to Mary Alice his main not-exactly-scientific achievement, and meeting her in 1953 "the most important (and fortunate) event in my life." During the early years of their marriage the Evanses lived on 8 acres of land on South Hill in Ithaca, New York, adjacent to Buttermilk Falls State Park, a home that became the inspiration for *Wasp Farm* (Evans, 1963), one of Howard's most successful books and a nominee for the National Book Award. With Mary Alice as senior author, they wrote a 363-page scholarly biography of Harvard entomologist William Morton Wheeler (Evans and Evans, 1970), a major figure of early twentieth-century science, whose story as recounted in the Evanses' biography gives a fascinating view of the issues, personages, and Old World influences that marked biology in the United States at the turn of the twentieth century.

I first met Howard Evans in 1966 when I was a graduate student. By that time he had moved from Cornell to Harvard, and I had an appointment to meet him in his office at the Harvard Museum of Comparative Zoology, the MCZ. I had heard that Evans was shy and reserved, a man of few words. What if we would end up having nothing to say? I soon found out that Howard Evans was the kindest and least pretentious of men, and he was not the least bit shy when it came to talking about insects. Later I learned that some people misinterpreted Howard's shyness as snobbishness. One person told me that she had ridden with Howard on the excruciatingly slow MCZ elevator many times over the space of an entire year without Howard ever saying a single word. He would just stare absently and wouldn't smile or attempt small talk. Those who knew Howard well, especially those who spent time with him in the field, learned that he was a person who was not embarrassed by silence.

When I went to the MCZ as Howard's postdoctoral associate in 1967 he was at the height of his productivity. The year before, 1966, had been what he later called his "banner year." In that single year he authored 10 publications, totaling well over 1,000 pages. They included his now classic synthetic review on "The Behavior Patterns of Solitary Wasps" (Evans, 1966a), a 526-page book on *The Comparative Ethology and Evolution of the Sand Wasps* (Evans, 1966b), and a 443-page monograph on the systematics of pompilid wasps (Evans, 1966c), an astounding list of achievements for one man in one year. In 1967 Howard was awarded the William J. Walker Prize of the Boston Museum of Science, for contributions to natural history.

In addition, he produced a constant stream of highquality popular works that did much to promote entomology and conservation in the public realm. He accomplished this prodigious output by dividing his workday strictly into two parts: While at the museum he did his "scientific" work and at home he did what he called his "literary work," meaning work on the essays and books that were outside his museum duties. At home he often played recorded music while working or relaxing. He would always leave his desk at the museum completely clear of clutter when he went home at the end of the day.

Some think that Howard's clean desk top was made possible by a set of messy drawers underneath, but I think it was the same orderly discipline that enabled him to accomplish large amounts of work and writing without pause for the 54 productive years spanned by his career. Whatever his secret for rapid publication, Howard never seemed pressured or nervous. He always had time for students. He never seemed too busy to write an encouraging letter to an amateur insect enthusiast, or to a kid hoping for a career in entomology.

E. O. Wilson recently told me the following story from those days at Harvard. When Howard was in his office he sat hidden from view behind a high bookcase, and the department secretary worked at a desk on the other side, near the door to the collection. If you came for department business you never knew whether Howard was present on the other side of the bookshelf, and if he ever listened to what went on there, he never let on. Ed Wilson decided to put this to the test by performing an experiment. He knew that Howard and Mary Alice were working on their biography of Wheeler, and that they had spent hours interviewing Wheeler's daughter Adaline. But there weren't many other people still around who had known Wheeler. So, to test Howard's quiet discretion, Ed walked in and said to the secretary, in a squeaky imitation of a 95-year-old voice, "I am a friend of Professor Wheeler, and I'd like to see him." Howard instantly popped into view, revealing himself to be as much an eavesdropper as anybody else.

Howard considered his move from Harvard to Colorado State University in Fort Collins in 1973 as one of the best things he ever did. Tired of the long commute between home and the museum, disillusioned with a new administration at the MCZ, and with good places for fieldwork diminishing in Massachusetts, the Evans family decided to move. As Howard put it, they decided not to give Harvard tenure.

Howard's unpublished autobiographical essay, "A Brief Review of Scientific Accomplishments," written when he turned 80 (in 1999), mentions that when the Evans family moved to Colorado State, he actually accepted a nontenured position! He had already published 170 papers and 6 books. Not surprisingly, he received tenure at CSU soon after he arrived. At Harvard, Howard had only one graduate student, Robert Matthews (now a professor at the University of Georgia). At CSU he served as advisor for several graduate students, including the late Byron Alexander (a CSU master's student who later studied with George Eickwort at Cornell), Darryl Gwynne, Mary Hathaway, Allan Hook, Rob Longair, Kevin O'Neill, and William Rubink. Three years after the move to Colorado, Howard was awarded the Daniel Giraud Elliot medal (in 1976) by the National Academy of Sciences, given for "recently published meritorious

work in zoology." A year later he was elected to the National Academy of Sciences. Howard says in his essay that he had "no illusions about these awards" and once in a letter he told me that he thought of dropping out of the Academy, which he called "an elitist club" that wasn't "his cup of tea," but that he kept his membership in the hope of helping to elect other field biologists to the Academy. He did regard election to the Academy as an important recognition, however. With characteristic modesty he mentions in the unpublished "Autobiographical Notes" written for his family that it was "an indication that I have done reasonably well as a scientist." By that time, at the age of 80, he had described a total of 782 new species of insects, plus 31 new genera, and even a new family: the Scolebythidae, a family of wasps found in the Southern Hemisphere. Ten of the new genera are based on study of fossils.

Evans was a pioneer in the use of behavioral data in systematics, and he proposed a number of important ideas that I would call "transition hypotheses" showing how complex behaviors such as nest building, social life, and specialized prey transport could have evolved from hypothesized ancestral states. Along with phylogenies and adaptive explanations in terms of natural selection, such hypotheses establishing the feasibility of particular phenotypic changes are an essential part of evolutionary explanations. Among his publications Howard was most proud not of the theoretical ones but of those packed with new data on natural history, such as his 1970 monograph on "Ecological-Behavioral Studies of the Wasps of Jackson Hole, Wyoming" (Evans, 1970). "I have always been especially proud of that paper," he wrote.

Some of Howard's ideas were far ahead of their time. He presented data on wasps that showed how behavior, including learning, could affect evolution, and he discussed the general importance of this especially in his 1966 book on sand wasps (see also Evans, 2002). Howard's ideas on how behavior can take the lead in evolution are now being cited more frequently than before, as evolutionary biologists are increasingly aware of how the condition sensitivity of organisms can supplement the genetic study of evolution. Howard saw that connection long ago, and because of it he wrote important critiques of overly gene-centered thinking, such as some analyses involving kin selection (e.g., see Evans, 1977). One paper he considered underappreciated described what he called dual sex-limited mimicry in South American spider wasps (Pompilidae), where he showed that in several species the males mimic social wasps, and females of the same species mimic tarantula hawks (*Pepsis*) (Evans, 1968b).

Howard Evans was never a powerful administrator or a biopolitician. He did not run a big lab bustling with technicians. He wasn't a brilliant orator, and he didn't hobnob with the rich and famous. Yet he was a leader among biologists and had a deep influence on those who knew him. He exerted a special kind of leadership in entomology because he stood for certain values in science and a certain kind of decency in human affairs. His way of promoting those values, aside from his personal interactions with the people around him and the quality of his scientific work, was to write clean, beautiful poetic prose that was at the same time lighthearted and earnest and deep. Three things stand out among the ideals that he promoted in both his scientific publications and his books and articles written for the general public. First, he stood for a love of nature, for the humble inhabitants of this planet, especially the insects, and he argued eloquently for their respect and preservation. Second, he stood for the value of curiosity-driven research, though it is worth mentioning that he never praised

pure science at the expense of the applied, for which he had an equal respect. "Curiosity," he wrote, "may have 'killed the cat,' but it has nourished every good scientist" (Evans, 1985, p. 23). Third, he defended the importance of research on natural history. He was incensed when he read in a book review that "biology is a system that proceeds from biochemistry to the associated subjects of neurophysiology and genetics. All else . . . is stamp collecting" (Evans, 1963, p. 149). "If this is so," Howard wrote, "I can lay no claim to being a biologist . . . I find Darwin, Gray, and Fabre worth emulating in this twentieth century." But Howard never allowed himself to be preachy and pedantic for very long. In the middle of this tirade about stamp collecting he says, "And it seems unfair to call me a stamp collector when I can never remember what it costs to send a postcard." With Howard Evans, science was serious but it was never too serious; there was always room to lighten up.

I was lucky enough to be working with this supremely humane man when I came up against the two greatest crises in the life of a woman in science: the birth of my first baby and the offer to my husband of an attractive job in a place where there would of course be no formal job for me. A lesser advisor than Howard—or perhaps I should say one with a less strong-minded wife than Mary Alice-might have given up on me then and there. But Howard never withdrew his support, even when I began to work mostly at home, and most of my projects began to lag, including my chapters for a book we were writing together on wasps (Evans and West-Eberhard, 1970). On the contrary, he recommended both my husband, William Eberhard, and me for a fellowship at a summer research station, even though we would be going there directly from a maternity clinic; and he waited with seemingly endless patience for my chapters of our book. Howard always treated us with respect as a couple, reinforcing our own natural optimism that we would both keep going in science, never turning his back when, in the eyes of others, the signs probably did not look too good.

Howard Evans was legendary among entomologists for his athletic prowess with an insect net. One of his students, Allan Hook, remembers that once while collecting at night in Australia he and Evans were trying to catch some hawk moths that were zipping up and down a trail. Allan couldn't come close to catching one even though he considers himself especially fast with a net, but Howard managed to get one. When he thrust his hand into the net to extract the specimen, he exclaimed, "Hey, it's hairy!" The elusive specimens were bats, and Howard was quick enough to catch one.

After Howard retired from his position at Colorado State in 1986, the Evanses moved to a beautiful mountain home 35 miles from Fort Collins. At 7,800 feet it had a spectacular 50-mile view on all sides. The view did not completely distract Howard from writing, and he completed five books and many scientific articles after his retirement. He continued to do fieldwork, and taxonomic research on collections, throughout the rest of his life.

Howard Evans's approach to science and nature was most completely stated in his book *Life on a Little-Known Planet* (1968a), where he concluded (p. 293), "The earth is a good place to live. We shall appreciate it more and more as we explore the moon and the planets. If man shall ever have another home, it is presently unimaginable. We had better learn to respect the little-known planet beneath our feet."

Howard Evans departed this little-known planet on July 18, 2002, at the age of 83, leaving life here a little better known than it was before he arrived. I think it is fair to say that he was one of the finest entomologists of all time. Not only was he the leading authority on the systematics of a

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number of large groups of insects but he also published widely on insect behavior, larval morphology, and insect paleontology. His pioneer analyses of behavioral and biological data, published in the 1950s and 1960s, contributed to a major change in how systematics was done. Howard Evans was a shy and unsentimental man, a man who treasured fieldwork in remote and beautiful places far from people, and who often, in good humor, compared humans unfavorably with cockroaches and fleas. But at the conclusion of the autobiographical sketch he wrote in 1999 he refers to the "sterling people" he knew during his career in biology, and says that knowing these people had been "the greatest reward" of his professional life. He was a fine colleague and a warm friend who is not just missed but is also irreplaceable in the lives of those who depended on his mastery of broad areas of entomology and his eloquent enthusiasm for research in natural history. A complete list of his 265 scientific papers, 17 books, book reviews, and popular articles has been published elsewhere (West-Eberhard, 2004).

PARTS OF THIS essay were presented as a lecture in the symposium "Life on a Little-Known Planet: A Tribute to Howard Ensign Evans," sponsored by the Entomological Society of America, Cincinnati, Ohio, on October 26, 2003. This biography is abstracted from a longer version published in the *Journal of the Kansas Entomological Society* (West-Eberhard, 2004). Mary Alice Evans provided a copy of the unpublished scientific autobiography of Howard Evans written in 1999, an essay of personal reminiscences written for his family in 1986, and a complete list of his publications. Arnold Menke provided the frontispiece, dated 1968, from a collection of portraits of noted sphecidologists printed by the U.S. Department of Agriculture in 1974.

REFERENCES

- Evans, H. E. 1951. The Song I Sing. Boston: Bruce Humphries.
- Evans, H. E. 1963. Wasp Farm. New York: Natural History Press, Doubleday. (Reprinted in paperback by Cornell University Press, 1985.)
- Evans, H. E. 1966a. The behavior patterns of solitary wasps. Annu. Rev. Entomol. 11:123-154.
- Evans, H. E. 1966b. The Comparative Ethology and Evolution of the Sand Wasps. Cambridge, Mass.: Harvard University Press.
- Evans, H. E. 1966c. A revision of the Mexican and Central American spider wasps of the subfamily Pompilinae (Hymenoptera: Pompilidae). Memoirs of the American Entomological Society No. 20.
- Evans, H. E. 1968a. Life on a Little-Known Planet. New York: Dutton.
- Evans, H. E. 1968b. Studies on neotropical Pompilidae (Hymenoptera). IV. Examples of dual sex-limited mimicry in *Chirodamus. Psyche* 75:1-22.
- Evans, H. E. 1970. Ecological-behavioral studies of the wasp of Jackson Hole, Wyoming. Bull. Mus. Comp. Zool. 140:451-511.
- Evans, H. E. 1977. Extrinsic versus intrinsic factors in the evolution of insect sociality. *Bioscience* 27:613-617.
- Evans, H. E. 1985. *The Pleasures of Entomology*. Washington, D.C.: Smithsonian Institution Press.
- Evans, H. E. 2002. A review of prey choice in bembicine sand wasps (Hymenoptera: Sphecidae). *Neotrop. Entomol.* 31(1):1-11.
- Evans, H. E., and R. W. Matthews. 1973. Systematics and nesting behavior of Australian *Bembix* sand wasps (Hymenoptera, Sphecidae). Memoirs of the American Entomological Institute No. 20.
- Evans, H. E., and M. J. West-Eberhard. 1970. *The Wasps*. Ann Arbor: University of Michigan Press.
- Evans, M. A., and H. E. Evans. 1970. William Morton Wheeler, Biologist. Cambridge, Mass.: Harvard University Press.
- West-Eberhard, M. J. 2004. Howard E. Evans: Known and little-known aspects of his life on the planet. J. Kansas Entomol. Soc. 77(4):296-322.

SELECTED BIBLIOGRAPHY

1950-1951

A taxonomic study of the Nearctic spider wasps belonging to the tribe Pompilini (Hymenoptera: Pompilidae). Parts I, II, III. *Trans. Am. Entomol. Soc.* 75:133-270; 76:207-361; 77:203-340.

1953

Comparative ethology and the systematics of spider wasps. *Syst. Zool.* 2:155-172.

1955

An ethological study of the digger wasp *Bembecinus neglectus*, with a review of the ethology of the genus. *Behaviour* 7:287-303.

1956

- Studies on the larvae of digger wasps (Hymenoptera: Sphecidae). Part I. Sphecinae. *Trans. Am. Entomol. Soc.* 81:131-153.
- With C. S. Lin. Studies on the larvae of digger wasps (Hymenoptera: Sphecidae). Part II. Nyssoninae. *Trans. Am. Entomol. Soc.* 82:35-66.

1957

Studies on the Comparative Ethology of Digger Wasps of the Genus Bembix. Ithaca, N.Y.: Cornell University Press.

1958

The evolution of social life in wasps. Proc. Xth Int. Congr. Entomol. 2:449-457.

1963

- The evolution of prey-carrying mechanisms in wasps. *Evolution* 16:468-483.
- A new family of wasps. Psyche 70:7-16.

1964

The classification and evolution of digger wasps as suggested by larval characters (Hymenoptera: Sphecoidea). *Entomol. News* 75:225-237.

A synopsis of the American Bethylidae (Hymenoptera, Aculeata). Bull. Mus. Comp. Zool. 132:1-222.

1966

- The behavior patterns of solitary wasps. Annu. Rev. Entomol. 11:123-154.
- A revision of the Mexican and Central American spider wasps of the subfamily Pompilinae (Hymenoptera: Pompilidae). Memoirs of the American Entomological Society No. 20.

The accessory burrows of digger wasps. Science 152:465-471.

The Comparative Ethology and Evolution of the Sand Wasps. Cambridge, Mass.: Harvard University Press.

1968

Studies on neotropical Pompilidae (Hymenoptera). IV. Examples of dual sex-limited mimicry in *Chirodamus. Psyche* 75:1-22.

1970

- With M. A. Evans. *William Morton Wheeler, Biologist.* Cambridge, Mass.: Harvard University Press.
- Ecological-behavioral studies of the wasps of Jackson Hole, Wyoming. Bull. Mus. Comp. Zool. 140:451-511.

1973

With R. W. Matthews. Systematics and nesting behavior of Australian *Bembix* sand wasps (Hymenoptera, Sphecidae). Memoirs of the American Entomological Institute No. 20.

1977

Extrinsic versus intrinsic factors in the evolution of insect sociality. *Bioscience* 27:613-617.

1978

- With K. M. O'Neil. Alternative mating strategies in the digger wasp *Philanthus zebratus* Cresson. Proc. Natl. Acad. Sci. U. S. A. 75:1901-1903.
- The Bethylidae of America north of Mexico. Memoirs of the American Entomological Society No. 27.

18

1984

With K. M. O'Neill. Alternative male mating tactics in *Bembecinus quinquespinosus* (Hymenoptera: Sphecidae): Correlations with size and color variation. *Behav. Ecol. Sociobiol.* 14:39-46.

1986

With A. W. Hook. Nesting behavior of Australian *Cerceris* digger wasps, with special reference to nest reutilization and nest sharing (Hymenoptera, Sphecidae). *Sociobiology* 11:275-302.

1996

With A. Shimizu. The evolution of nest building and communal nesting in Ageniellini (Insecta: Hymenoptera: Pompilidae). J. Nat. Hist. 30:1633-1648.

2002

A review of prey choice in bembicine sand wasps (Hymenoptera: Sphecidae). *Neotrop. Entomol.* 31:1-11.