Connecting the Dots

Extending her initial studies of social wasps, Mary Jane West-Eberhard has spent her career probing the evolutionary relationship between social behavior and developmental flexibility.

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In 2003, Mary Jane West-Eberhard published *Developmental Plasticity and Evolution*, the culmination of many years of reflection and observation on the links between developmental biology and evolution. The seeds of this book had been planted 40 years earlier, when West-Eberhard was an earnest zoology undergraduate student at the University of Michigan.

In 1961, as a junior in college, West-Eberhard wrote a research paper for a class taught by entomologist Richard Alexander—who would later become her doctoral advisor—on the evolution of dance communication in honeybees.

Forager honeybees perform a "waggle dance" in the shape of a figure eight to communicate information to their colony mates about the direction and distance to nectar and water sources. Digging through studies of insect movement, West-Eberhard came across a University of Michigan thesis on movements of hemipteran insects—the true bugs. The student had observed that bugs placed in a maze would alternate between turning right and left—which he called "twig behavior" because it allows insects to reach an end of a branched twig. West-Eberhard proposed that honeybees performing the waggle dance employed this twig behavior, providing an example of an ancient phenotype being used in a new context.

Although her paper was never officially published, West-Eberhard used this undergraduate research in her book to illustrate the point that novel phenotypes can arise by reorganizing an existing gene-expression pattern. The reshuffling of functional behaviors to create new ones has now been well established through molecular biology studies and comparative research on behavior, says West-Eberhard.

> "I have not been a pure theorist. Pure theory only interests me if that theory can be tested and applied to real organisms in nature."

As an entomologist, evolutionary biologist, and theoretician, West-Eberhard has made a career of piecing together data and concepts that were previously thought to be unrelated. "I always get excited when I am putting things together that people do not usually connect," she says.

Here, West-Eberhard discusses how science has fostered her lifelong curiosity, how she prefers to develop ideas on her own, and how she continues to make connections others may not notice.

West-Eberhard wends Her Way

Inquisitive child. West-Eberhard recalls lively discussions around the dinner table, during which her father and mother allowed their children to speak their minds. "Growing up, I had parents who didn't mind a kid asking questions and took my questions seriously. They encouraged our curiosity, our taking part in family discussions," she says. "They were not scientists but they set the groundwork for my curiosity-driven research—which is basically what basic science is."

Bug roots. West-Eberhard belonged to a 4-H club in high school. "I loved the outdoors and always wanted to be a farm kid," she recalls. "We did this unusual entomology project, learning how to pin insects and create a collection. What I really wanted was a horse or a steer, but I had to settle for insects instead!"

Concrete concepts and connections. As an honors student at the University of Michigan, West-Eberhard took a zoology course with Alexander, an entomologist with a wide-ranging curiosity. "He taught us concepts instead of putting a lot of emphasis on memorizing facts," she says. When West-Eberhard needed a part-time job she sought out Alexander, whose office turned out to be in the university's Museum of Zoology. "I told him about my entomology projects through the 4-H club, so maybe that helped me get the job at the museum, which became really important to my career."

At home with biology. At the zoology museum, West-Eberhard felt more at home with the biologists than with their humanities counterparts, whom she had initially admired. The down-to-earth attitudes of field biologists influenced her decision to major in zoology, she says. "As an earnest Midwestern kid, I sometimes had discouraging experiences in humanities classes. I found there was a premium on sophistication in these circles that I just didn't have, coming from a small town in southeastern Michigan. But when I was around biologists, I was comfortable—my questions and curiosity were seen as something positive."

West-Eberhard Works

Watching wasps. West-Eberhard stayed at the University of Michigan to pursue a PhD in zoology with Alexander as her advisor. She expanded on her undergraduate research focus, studying the social behavior of wasps of the genus *Polistes*. Her fieldwork involved observing both individual and colony development, tracking the wasps from egg to adulthood. "I was interested in how different colony individuals ended up in different social roles," says West-Eberhard.

Serendipity. During the summer before her second year in graduate school, West-Eberhard ran into a Spanish-speaking student she had previously helped with English and with lab-report writing who turned out to be head of the biology department at Universidad del Valle in Cali, Colombia. He arranged for her to spend a field season in Colombia, where she studied tropical *Polistes* species. "I had been dreaming of going to the tropics," says West-Eberhard. Since most researchers were men, women had limited choices for field trips. "Women complicated things. People thought that it was not proper to go into the field with a group of men—we would need a separate tent and would change the whole atmosphere of the trip. So it was quite an adventure to undertake a tropical field trip on my own, but that was the only possibility at the time. Those five months in Colombia were very exciting for me. I had never even flown on an airplane before, and had to learn Spanish from scratch."

Kin selection. While West-Eberhard was in the field in Colombia, W.D. Hamilton published his seminal kin-selection paper, which contained the revolutionary proposal that evolutionary strategies favoring the reproductive success of an organism's close genetic relatives, even at that individual's own expense, enhance the reproductive fitness of the whole family or lineage. "Kin selection became one of the most important theories in evolutionary biology in the last century," says West-Eberhard. She used Hamilton's theoretical framework for her doctoral thesis, in which she compared the social behavior of the Michigan and Colombian social wasps. Through her fieldwork, she provided evidence that nongenetic, environmental factors that affected the costs and benefits of social aid were a major part of kin selection. West-Eberhard observed that behavioral differences among colony members were affected not just by genetic differences but also as a result of nutrition and social relationships.

Education approaches. West-Eberhard moved to Harvard in 1967 to do a postdoc with entomologist and insect ethologist Howard Evans, with whom she coauthored the book *The Wasps*, a comprehensive evolutionary study of both solitary and social wasp species. "My training at Michigan turned out to be more rigorous regarding foreign languages and scientific writing than what I saw of the training of Harvard graduate students. But it was an exciting place to be because there was so much important work going on. There was a lot of enthusiasm for natural history in the Museum of Comparative Zoology, where Evans, Ed [E.O.] Wilson, Ernst Mayr, and others who encouraged research in evolutionary biology were based," she says.

From practice to theory. After completing her postdoc, West-Eberhard, with her husband, William Eberhard, a biologist she met at Harvard, moved back to the tropics, first to Cali, Colombia, and then to Costa Rica. She continued to study the evolution and development of social behavior, specifically how female wasps take on defined roles within a colony. During the 10 years she spent in Cali, West-Eberhard began to extend her wasp research beyond kin selection theory and the evolution of the social behaviors of insects to environmentally mediated polymorphisms and social selection in general.

Extending Darwin's ideas. In *On the Origin of Species*, Darwin developed his theory of natural selection, only briefly addressing the idea of sexual selection, which he considered at length in *The Descent of Man* a dozen years later. "Sexual selection has to do with social interactions that couldn't be explained by natural selection, like the peacock's tail, which was strictly for winning a mate," says West-Eberhard. She argued for an extension of Darwin's theory, stating that sexual selection belonged within the larger category of social selection, including social competition among insects that use pheromones and other signals to communicate aggressiveness, and even baby chicks that cheep loudly and display bright faces and beaks to compete for parental attention. Like the peacock's tail, these are traits that allow an organism to compete for attention within a social group, West-Eberhard says.

Creative freedom. In 1979, West-Eberhard moved with her family to Costa Rica, where she worked out of the University of Costa Rica as a scientist with the Smithsonian Tropical Research Institute (STRI) until her retirement last year. "It takes a lot of time to put ideas together with evidence," she says. "The work I have done has been possible because of this Smithsonian position, which has given me time to think and to not be distracted by grant writing or the pressure of having to publish a lot of short papers."

Flexibility. Some of West-Eberhard's recent publications show how the ability of organisms to respond to

their environments can affect their genetic evolution. Divergent developmental pathways influenced by environmental cues and materials involve different patterns of gene expression, and "it is the expressed genes that are seen by selection," says West-Eberhard. Thinking about this concept led West-Eberhard to write her 2003 book on developmental plasticity and evolution. The book combines molecular, physiological, morphological, and behavioral evidence to posit that evolution mostly occurs through the reorganization of already established phenotypes or traits, rather than through an accumulation of new mutations.

From theory to practice. "My contribution to evolutionary biology has been to merge together theoretical concepts with data. I have not been a pure theorist. Pure theory only interests me if that theory can be tested and applied to real organisms in nature."

New directions. Several years ago, West-Eberhard was invited to give a plenary talk on the fetal causes of adult obesity. She had become interested in a theory proposed by medical researchers that linked fetal nutrition to adult obesity and diabetes. She is now digging into human evolution and into medical literature on diabetes and obesity. "The evolutionary explanations for modern obesity have some important shortcomings, and I am now trying to remedy those. This is, again, a chance to make some new connections, which is exciting. It is also exciting because of the importance of the topic for alleviating human misery and controlling the costs of public health, especially in developing countries."

West-Eberhard Wisdom

Human Rights. For many years, West-Eberhard has been an active member of the Committee on Human Rights of the US National Academy of Sciences, the Academy of Engineering, and the Institute of Medicine. "Freedom of expression is a basic requirement of science, and this committee is dedicated to cases around the world where that right has been violated, sometimes with shocking treatment of colleagues who have never advocated violence," she says. According to West-Eberhard, the committee works quietly, and sometimes very effectively, to urge the release of colleagues who are prisoners of conscience—those who are imprisoned for holding political or religious views that are not tolerated by their own governments—and who are often victims of extreme and unjust mistreatment.

Independent ways. "One of the reasons I was drawn to working with Alexander is that he really encouraged independent thinking. Perhaps it is a character defect in a way, but I would rather work on something on my own, because I like the freedom to develop and make my own conclusions."

Personalized kin selection. "I have always wanted to be independent, but at the same time, I have had lots of help from others," says West-Eberhard. Her parents visited her and her family repeatedly both during her first field trip to Cali and later, when she settled in Colombia and Costa Rica with her husband, who studies tropical arthropods, and their children. "They used to come and stay with the kids and my husband so I could go and travel long distance to a conference. Sometimes I would stay away for a while to work, and they would stay and fill in. They loved it, and it was a great help."

From student to editor. "My husband reads everything I write. I completely depend on him to be utterly critical of my work. What's funny is that I think I taught him how to write when he was a graduate student at Harvard because he didn't have the training I did on how to write scientific papers. In exchange for that, I got a lifetime of help with my own writing. Now he has published far more than I have!"

Greatest Hits

- Connected fieldwork observations to major evolutionary concepts such as kin selection, sexual selection, speciation, and the origins of new adaptive traits.
- From fieldwork on social wasps, linked animal social behavior to evolution, and particularly to kin selection theory.
- Provided a link between sexual and social selection and evolution, showing that social behaviors confer competitive advantages.
- Established the importance of the ability of organisms to respond to changes in their environment as part of an adaptive evolutionary process that results in gradual change, based on preexisting genetic variations in a population, called genetic accommodation.
- Published *Developmental Plasticity and Evolution* in 2003, which links organismal development with the genetic theories of evolution, and which has influenced how biologists view evolution.

Tags

social selection, social insects, sexual selection, kin selection, evolution, environment, entomology and developmental plasticity

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