PNAS PROFILE

Profile of Spencer C.H. Barrett

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Spencer Barrett's career uncovering the evolutionary underpinnings of plant reproduction reads like an adventure story, featuring a trip through Africa and a treasure hunt in Brazil. A botanist and evolutionary biologist at the University of Toronto, Barrett travels the world collecting plants and testing evolutionary hypotheses through observations and experiments. Barrett's specialty is the evolution of flowering plant reproductive systems, with a focus on how and why mating system transitions occur. He has helped rejuvenate the field of plant reproductive biology, integrating ecological and genetic approaches and promoting microevolutionary studies of variation in reproductive traits. Among his contributions, Barrett has shown that the interplay between pollinators and floral displays affects mating patterns, that many features of flower design function by increasing the effectiveness of pollen dispersal and receipt, and that invasive plants can evolve rapid adaptations to novel environments. His inaugural article (1) expands on his work on floral evolution by demonstrating how changes in elevation affect pollinator service and mating patterns in a subalpine primrose.

Spencer C.H. Barrett conducting fieldwork in the Pantanal wetlands of Brazil. Image credit: Suzanne Barrett.

Learning by Doing

Barrett grew up in the London suburb of Pinner in England. His father, an electrical engineer, encouraged an early interest in science, taking him to natural history and science museums in London and plying him with science books. Even more influential was the family garden with greenhouses full of flowers and an allotment where the family grew much of its food.

"I remember boring times on holidays in Cornwall when my father wanted to visit nurseries, whereas I wanted to play on the beach," he says. "But even if it was unconscious, an appreciation for flower diversity must have sunk in."

Barrett also spent hours tromping through local woods, collecting insects, watching birds, and finding and naming plants. Barrett's grammar school biology teacher, Muriel Hosking, cultivated his passion for plants. She would pick up Barrett and classmates in her van to go badger-watching at night with flashlights. She encouraged Barrett to apply to university, and with his parents' support, he went to the University of Reading, which had a program in plant diversity. In 1968, as he worked toward a degree in horticultural botany, the chair of his department, agronomist Arthur Bunting, asked Barrett and classmates if anyone wanted to spend the following year doing research abroad. Barrett asked to go to Africa.

"Bunting allowed us to dream," says Barrett "and he had a network of colleagues all over the world." Bunting placed Barrett at the Swaziland Irrigation Scheme, and Barrett left for Africa on July 21, 1969, the day Neil Armstrong walked on the moon. Having no real research experience, Barrett worked on ways to tackle infestations of a wild and weedy rice in cultivated rice fields. While in Swaziland, Barrett collected plant specimens to bring back to the herbarium at the Royal Botanic Gardens at Kew. When his year was up, he spent several months traveling through Africa, staying with Bunting's acquaintances, including the Leakey family in Kenya. "I met some really interesting people, thanks to Bunting," he says. "When I got back, I knew I wanted to do graduate work and be a researcher."

Winding Path

Back at Reading, crop evolutionist Barbara Pickersgill became another important mentor. She worked with Bunting to secure funding for an expedition to search for wild cotton in northeast Brazil. The expedition's aim was to prove that seeds from a wild African cotton with fibers (lint) had floated across the Atlantic Ocean to Brazil, bringing the first linted cottons to the New World. The team set off in January 1972 and, after many hours of fruitless searching, discovered three locations of a species of wild linted cotton (2). The expedition spurred Barrett's interest in plant exploration, and his

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experience in Brazil was influential when later he returned to the Amazon basin.

Pickersgill did her doctoral work at the University of Indiana and encouraged Barrett to pursue graduate studies in the United States, emphasizing the importance of picking a top researcher rather than just a program. For Barrett that person was Herbert Baker of the University of California, Berkeley, a prominent plant evolutionary ecologist and colleague of the eminent evolutionist G. Ledyard Stebbins. Barrett had read a book they coedited, "The Genetics of Colonizing Species," based on a 1965 symposium of leading evolutionary biologists and ecologists. "What really influenced me was that they taped the discussions after each presentation and included them at the end of each chapter, and the exchanges identified so many interesting questions," says Barrett, who, with colleagues, recently organized a similar symposium and edited a 50th anniversary book "Invasion Genetics" including the discussion questions and answers (3).

Baker accepted Barrett into his laboratory and encouraged him to forge his own path. Barrett wanted to study weed evolution in agricultural settings and started work in California's Central Valley. The effort led to work on rice weeds that have evolved to evade detection by mimicking the appearance of domesticated rice (4). Subsequently, Barrett found an opportunity to work on rice weeds in the Amazon, where he fell in love with water hyacinth, a species native to Brazil that is now invasive in aquatic habitats around the world. Barrett knew about an unsolved botanical mystery concerning the flowers of water hyacinth and dating back to Darwin's book on plant sexual diversity. Darwin was sent pressed flowers from Brazil of two different water hyacinth flower forms: one with long styles and one with midlength styles. However, based on the positions of their stamens, Darwin predicted that there should also be a third form with short styles. By luck, Barrett found it in a drainage canal (5) along with a new thesis topic: sexual polymorphisms in plants.

Barrett developed a fascination for the diverse ways in which plants mate. Some plants are entirely cross-fertilized; others are largely self-fertilized, and still others use both modes of fertilization. Floral diversity can be equally intriguing; for example, water hyacinth is sexually polymorphic with three floral forms (tristyly), whereas the garden primrose has two floral forms (distyly). When pollinators are abundant, these heterostylous polymorphisms function to promote cross-pollination, as Barrett later demonstrated experimentally (6). His thesis focused on the evolution and breakdown of heterostyly in water hyacinth and close relatives (7). Since then, he has continued to work on understanding how this complicated sexual system can become destabilized, transitioning from cross- to self-fertilization, often because of a lack of suitable pollinators (8).

With a year to go on his doctorate, Barrett heard that the University of Toronto was hiring an ecological geneticist. Barrett applied, secured the position, and started working as a lecturer and researcher in 1977—even before finishing his thesis, which he had to complete alongside teaching. "It was awful," he recalls. Yet Toronto was a good fit for him and his wife, especially once they started a family. It helps, he says, that they travel for work, spending part of the Canadian winter with collaborators in warmer climates including Brazil, Australia, Chile, and China.

Integrating Pollination and Mating Biology

In Toronto, Barrett started to collaborate with pollination biologist Lawrence Harder, who is now at the University of Calgary. The duo recognized that plant reproductive biology was largely subdivided into two fields with little cross talk. Pollination biologists were mainly field ecologists studying pollinator behavior and how it influences the quantity and quality of the pollen dispersed. In contrast, researchers studying mating were often laboratory based, developing genetic markers to identify mating partners and quantify mating, mostly ignoring the pollination process. Yet pollination and mating are inextricably linked.

A sabbatical year at the Commonwealth Scientific and Industrial Research Organization in Canberra, Australia, in 1983 solidified Barrett's determination that reproductive biology could only mature by integrating information on both pollination and mating through ecological and genetic approaches. "A few of us argued that it's not enough to visit a population once and collect seeds and then look at their genetics," he says. "We needed to know about the ecological context of pollination in order to understand mating patterns." He also realized that plant paternity was as important to overall fitness as plant maternity. Most plants are hermaphroditic, and determining how much cross- and self-fertilization occurs and the paternity of seeds requires genetic markers. Harder and Barrett's 1995 paper in Nature (9) was a breakthrough in integrating pollination and mating. Performing experiments in Barrett's garden in Toronto, the duo used genetic markers to demonstrate that male fertility suffers in plants with large floral displays because pollinators move from flower to flower on a single plant, leading to self-fertilization rather than male siring success.

Transitions

Barrett explains his 45-year career at the University of Toronto as being primarily focused on understanding evolutionary transitions in plant reproductive systems. He gained inspiration from the New Zealand botanist David Lloyd, an influential mentor (10). During this time, Barrett has made important contributions to three of the major transitions in plant reproductive systems, including why plants evolved self-fertilization from cross-fertilization and the related genomic consequences (11), the evolution of separate sexes from hermaphroditism (12), and, recently, the mechanisms responsible for the evolution of wind pollination from animal pollination (13).

Barrett's inaugural article (1) continues his work on transitions, specifically how pollination environments affect mating patterns. The study was conducted in China, where Barrett and Harder have held workshops for the past 20 years, training Chinese students in plant reproductive biology field research. Working with doctoral student Shuai Yuan, the team examined how changes in elevation influence pollination and mating in primrose populations. At low elevations with abundant pollinators, populations are distylous, having two forms that mate with one another. At medium elevations, there are fewer pollinators. “So the mating system becomes destabilized,” says Barrett. “It still works to some extent, but it’s not functioning in the way Darwin predicted.” At high elevations, plants mostly mate with themselves because there are few pollinators. “It’s a great example of a shift in mating occurring within a species where we understand the ecological mechanisms involved,” he says. “The quantity and the quality of pollinators change as you go upslope, and populations respond by evolving different floral traits and mating systems.”

These days, Barrett, now an emeritus professor at the University of Toronto, spends his time in the Western Cape of South Africa working on the evolution of mirror-image flowers (14)—a project funded by a three-year grant from the Human Frontier Science Program. He may be slowing down, he concedes, but his curiosity to explore flower diversity is unflagging.

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