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EARLY HISTORY AND PROGRESS OF WOMEN ECOLOGISTS: Emphasis Upon Research Contributions

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ABSTRACT

Although women are increasingly prominent as ecologists, a report on their progress through the history of ecology in overcoming personal and societal obstacles provides interesting insights regarding their research achievements. Selected, predominantly American, women ecologists are presented within five time frames according to the date of their PhD, an event marking the beginning of their careers. A general view is given for pre-1900 Protoecologists, followed by brief professional sketches for 10 Early Pioneers (1900–1934), 16 Late Pioneers (1935–1960), and 28 members of the First Modern Wave (1961–1975). The relatively large number of women who earned doctorates after 1975 precludes discussion of individuals from this time in this review. The following issues are discussed in the context of their research contributions: 1) motivating factors, 2) graduate education and subfield entered, 3) mentors and role models, 4) employment, 5) marriage and family constraints, and 6) recognition. These issues are compared with data from recent surveys for post-1976 women doctorates. Each selected woman still alive was contacted for her assessment of her research; 156 research citations display the significance and range of subjects studied. A steady, albeit slow, progress since 1900 is evident, although some problems regarding gender equality in professional development of women ecologists persist. These issues, however, are now more clearly recognized and addressed.

INTRODUCTION

In 1988 I hoped that there would be no further need to discuss the contributions of women ecologists because we would be recognized just as ecologists

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(81). Although women have become increasingly prominent as ecologists, it still seems timely and useful to consider the progress women ecologists have made in overcoming both personal and societal obstacles, particularly with regard to research contributions. Citations exemplifying their research reveal the significance of women's contributions and the extraordinary range of subjects studied.

Women ecologists clearly, albeit somewhat slowly, have made progress since the beginnings of "self-conscious ecology" (100, 106) near the turn of the century. Initially, they took the opportunities to obtain advanced degrees and used these primarily to teach, although a few succeeded in doing research. The percentage of women obtaining doctoral degrees dropped through the 1930 depression years, the 1940 war years, and the 1950 postwar years. However, some now-influential women ecologists persisted to obtain doctorates through these difficult years. Following the coincidence of the environmental and women's movements in the 1960s and 1970s, the number of women ecologists with doctorates increased as did the positions they obtained in major institutions. Thus these women had increased opportunities to influence ecology through their own research and by having their own doctoral students and postdoctoral fellows at research-oriented universities. Furthermore, the numbers that have received prestigious awards and assumed leadership roles in various professional societies have increased. I discuss the obstacles these successful women have overcome in achieving this status.

Ecology is a notoriously heterogeneous field, and boundaries are even more difficult to define before the recognition of self-conscious ecology in 1894 (100, 106). However, I thought it appropriate to include a few women naturalists from the nineteenth century as "protoecologists" (106). Following general discussion of this pre-1900 period, I emphasize a selected group of women ecologists who obtained PhD degrees before 1976. The large burst of women with doctorates who followed allows in this paper only a general evaluation of their progress, rather than a continued discussion of their individual contributions. Although most of the women discussed are Americans, a few are British and Canadian. To facilitate a sense of progression, the women are grouped in five time frames according to the date they obtained their PhD degrees, an event marking the beginning of a professional career. I communicated with the living ecologists to obtain data regarding them; the significance of their research is derived from their own assessment and suggestions from others working in their subfields.

In the context of their research contributions, the following issues are discussed using different women as examples: 1) motivation to study and to disseminate ecological information (by teaching and/or research), 2) availability of graduate education and the emphasis in subfields, 3) mentors and role models as motivators and/or providers of support, 4) employment, such as availability of jobs at major institutions in which a high level of research is possible, 5) family constraints on careers, and 6) recognition of contributions by election as officers of scientific societies and selection for prestigious awards. Some of these issues are compared with data from a 1987 survey of 200 women (81) and from recent publications that consider various aspects of women ecologists' careers. I conclude by evaluating progress through time.

PRE-1900 PROTOECOLOGISTS AND CONSERVATIONISTS

Women traveled around the world to study natural history during the seventeenth, eighteenth, and nineteenth centuries, e.g. Englishwoman Mary Kingsley (91). Discussion of this period is limited, partially because the exploits of these courageous and adventuresome women should receive separate attention. Bonta (14, 15) points out that natural history studies by American women, even if published, "had been overlooked in standard chronicles of natural history because of women's position in society during the eighteenth, nineteenth, and early twentieth century. Women were viewed as amateurs, even though professional men in the same fields who had achieved great renown often had the same amount or even less professional training than the women" (14, p. xiv).

The seventeenth and eighteenth century exploits of Maria Sibylla Merian are amazing. After divorcing her husband, she obtained a grant from the city of Amsterdam and at age 52 traveled with her daughter to Surinam to illustrate tropical plants and insects; she published her insightful ideas on metamorphosis of insects along with beautifully engraved plates in 1705 and 1719 (110). She had previously published three volumes [1679, 1683, and 1719] on *The Wonderful Transformation of Caterpillars and (Their) Singular Plant Nourishment.* However, because she unfortunately did not integrate her discoveries into the existing body of scientific knowledge she has been considered a "connoisseur rather than an investigator of metamorphoses" (63, p. 22). Her accomplishments are the more incredible because women even in the nineteenth century had difficulty publishing anything other than popularized observations.[1]

Outstanding among women in the nineteenth century who clearly projected her ideas is Ellen Swallow (Richards), whom Robert Clarke identifies as "the

[1]Hutchinson (64) points out that women who studied field natural history in Ireland during the nineteenth century did not publish under their own names. For example, although Mary Bell discovered stridulation in the corixid water bugs—a group of insects that produce sound under water, a process that has complicated functional significance in sexual isolation—her papers were published under her brother's name in 1845 and 1846. Hutchinson (64) suggests that the brother's failure to mention his sister's name was probably related to his feeling that it was immodest for a woman to publish.

woman who founded ecology" (30, title). Swallow, a pioneer woman chemist with a BA from Vassar in 1870, was the first woman admitted to MIT as a special student. She then, with the support of her MIT professor husband, opened the Women's Laboratory there. In 1892 she presented the idea of "oekology"' as an interdisciplinary science concerned with industrial health and water quality, thus anticipating the applied ecological studies of professional ecologists since the 1960s. Her ideas received little attention when in 1894 ecology was formally defined (dropping the initial "o" in the term) as a subdiscipline of plant physiology that emphasized adaptations of organisms to the natural environment (100).

Some early influential ecologists, such as Frederic Clements and Victor Shelford, however, did pose key questions regarding the impact of humans on the natural environment. American women also developed interests and organizations during the late nineteenth century that paved the way for women's prominence in conservation activities during the early twentieth century (109). Literary clubs brought women together, and women's rights movements exposed them to the political process. Leisure time also gave middle- and upper-class women opportunities for botanizing, gardening, bird lore, etc. Some of these women not only recorded their observations on nature, they also wrote articles in a variety of journals encouraging the public to conserve the wonders of nature (15).

Nationally, the General Federation of Women's Clubs, founded in 1890, actively informed women about urgent political, economic and social issues of the day, including environmental concerns. Women were also involved early (starting in 1886) in Audubon Society activities, such as protection of game birds from hunters and protection of plumed birds from extinction due to ladies' fashions. They became particularly active with regard to forestry. For example, recognizing the need for trained men to manage and protect the forests, the women of the California Club in 1903 presented a bill to the state legislature to establish a School of Forestry at the University of California, Berkeley. At that time the only three schools of forestry in the United States were on the East Coast.

"Although the women of the organizations represented at the National Conservation Congresses were public activists in their local communities, they nevertheless accepted the traditional sex roles assigned to them by the late nineteenth century American society as caretakers of the nation's homes, husbands and offspring . . . " (109, p. 73). The outstanding achievement of many of these women in bringing to the public the need for preserving the environment was a prelude to the extensive conservation activities of many women who obtained PhDs and managed to secure professional positions in ecology.

1900–1934 DEGREES: EARLY PIONEERS

Near the turn of the nineteenth century women broke through barriers to graduate education in science (154). Simultaneously, universities such as Illinois, Chicago, Nebraska, Minnesota, and Cornell became centers for the new field of ecology. Although some women were actively involved only in volunteer conservation activity, other women in these early days were obtaining a high percentage of the PhD degrees in ecology, e.g. 100% of pre-1920s PhDs, and 50% of those between 1920 and 1929, at the University of Illinois (M Willson, personal communication), and 50% of the pre-1920 doctorates at Cornell (B Peckarsky, personal communication). These are particularly significant figures considering that women did not get suffrage in the United States until 1920.

Women Associated with Research Sponsored by the Carnegie Institution of Washington

Edith Schwartz Clements and Edith Bellamy Shreve are better known for their activities in ecology than are many others who earned degrees just after the turn of the century; they may have become so visible partially because of their famous ecologist husbands. The greater part of their husbands' research was carried out under the auspices of Carnegie Institute of Washington (CIW), a private foundation whose funding has played a significant role in physiological and ecological studies since the turn of the century. These women's research contributions to ecology, however, are quite distinct from one another.

Frederic Clements encouraged Edith Schwartz to do graduate work under his direction (33). With a substantial autecological dissertation on "The Relation of Leaf Structure to Physical Factors," in 1904 she was the first woman to obtain a PhD in botany (as well as ecology) at the University of Nebraska. Edith and Frederic were married in 1899, and after finishing her degree, she became the exemplary helpmate in all aspects of his research. They both preferred being and working together to being separated. In fact, in the 46 years of marriage the Clements were separated only once for more than a few hours (164). Although Edith's dissertation was her only research publication per se (31), because she chose to devote most of her energies to assisting with her husband's work, she utilized her talents in botanical illustration, publishing several books of flower paintings (e.g. 32). She also compiled and edited (with BW Allred) *Dynamics of Vegetation* (2), published after Frederic's death in 1949, and she wrote a book about the Clements' adventures together in the field (33). Frederic apparently recognized Edith's potential as an ecologist in her own right in his comments to the South African ecologist John Philips, "Mrs. Clements would hold that position today . . . [like that of Dr. Philips near the top of the world's ecologists] . . . had she not devoted herself to furthering my career instead of winning recognition as an ecologist in her own right" (164, p. 242).

Frances Louise Long, another of Frederic Clements' students, took her baccalaureate at Nebraska and her PhD (1917) at the University of Minnesota when Clements moved there. She published her PhD dissertation on the quantitative determination of photosynthesis (94), a topic indicating the importance Clements ascribed to physiological studies in ecology. When Clements moved to CIW in 1918, Long became a research associate there, and they continued their research collaboration, coauthoring several significant volumes on topics such as pollination and adaptation in plants (34, 35). When Frederic received his CIW appointment, Edith remarked that he would also be allowed a (paid) assistant, but a "'mere wife' would work just as hard for nothing" (164, p. 243). Thus was the difference in professional status between Edith Clements and Frances Long.

Edith Bellamy Shreve worked professionally within the framework of her marriage in a very different way and more daringly for her time than did Edith Clements (16). She took her baccalaureate at the University of Chicago in 1902 in chemistry and physics, but never completed her PhD. She then taught physics at Goucher College, where she met Forrest Shreve, who taught botany there. Shortly after their marriage in 1909, they went to the CIW's Desert Research Laboratory in Arizona. Edith accompanied her husband to study distribution of desert vegetation, until the birth of their daughter in 1918. Although it is not known how much she contributed to Forrest's work, sometime in those early years Edith decided to pursue a career of her own. In so doing, she confronted stereotyped ideas of "women's work" and also had to fight the widespread prejudice against married women working independently. Her husband, however, was for that time unusually supportive. Forrest's biographer (17) suggests that his egalitarian attitude probably came from a Quaker upbringing; his mother was also college educated, and he apparently did not feel threatened by a wife with independent achievements.

Edith Shreves' background in the physical sciences led her (after some tutelage from Burton Livingston at Johns Hopkins University and encouragement from DT McDougal, Director of the CIW Desert Laboratory) toward plant physiological studies in what would now be considered physiological ecology. Edith was an experimentalist; most of her studies were conducted under controlled conditions in the laboratory. She was an imaginative, dedicated, and independent-thinking researcher who published papers on the autonomic movements in cactus (cholla joints). She discovered that the plants apparently lost water during the night and took up water during the day, the opposite of patterns expected in 1915 (157). Her continued attempts to understand the mechanisms led her to the verge of discovering crassulacean acid metabolism, a specialized mode of photosynthesis in cactus and other succulents. She also worked on methods for determining leaf temperature and transpiration (e.g. 158, 159), and she produced a significant study of seasonal water relations in desert plants (160).

Early Women in the Chicago-Cowles Genealogy

To trace the origins of several generations of female ecologists that span the time 1900–1975, I describe the major pedagogical genealogy of plant ecologists influenced by HC Cowles at the University of Chicago at the turn of the century. Cowles founded the "School of Physiographic Ecology," which linked long-term landscape changes to vegetational change and emphasized the importance of physiology. This genealogy further shows the role that prominent male ecologists (e.g. Shelford, Cooper, Oosting, Buell, Billings, Marr, and Mooney) played at an ever-increasing number of universities in supporting women who have become prominent contributors to ecology.

Although Emma Lucy Braun took her PhD at the University of Cincinnati in 1914, she was so influenced by Cowlesian views (her dissertation topic was "The Physiographic Ecology of the Cincinnati Region") that she has been included on this pedagogical tree. Braun's interest in ecology was stimulated by her schoolteacher parents, who took their close-knit family to explore forests around Cincinnati. Her older sister Annette was a distinguished entomologist, and the two sisters lived and worked together. This not only provided mutual support but made possible their extensive field studies throughout the eastern deciduous forest. Together they dealt effectively, at a time when women field scientists were uncommon, with such problems as moonshiners and the "backwoods" conditions in the Appalachian Mountains.

Lucy Braun's professional career was also at the University of Cincinnati. She became an Assistant Professor of Botany in 1925 and rose to Professor of Plant Ecology in 1946. She retired in 1948 to have more time for her research and was granted an honorary Doctor of Science degree by the University in 1964. Contrary to the usual situation for women faculty at the time, Braun had 13 MA students and one PhD. Nine of the MA degrees were earned by women; several of their theses were published, but information is not available about the women's careers.

Braun published prolifically, and there was an air of independence in her publications: She was sole author of four books and 180 articles in 20 journals. Her research "coincided with the time when the field of plant ecology was becoming recognized as a scientific discipline" (175, p. 83). In fact, her research was hailed as "instrumental in the development of that discipline;" one of her greatest achievements was her monumental book in 1950, *Deciduous Forests of*

Eastern North America (19), in which many of her significant journal articles are referenced. It represents 25 years of field work, initially in specific areas, followed by traveling 65,000 miles during the last 10–15 years to know the deciduous forest as a whole. Fosberg (55, p.67) wrote "one can only say that it is a definitive work, and that it has reached a level of excellence seldom or never before attained in American ecology or vegetation science, at least in any work of comparable importance." This remarkable woman was constantly a "first woman," e.g. the first woman officer of the Ecological Society of America (ESA)—Vice President (1935) and President (1950)—and the first woman to have an ESA award named in her honor (Braun Award for Excellence in Ecology). She was given the Pope Medal by the Cranbrook Institute of Science as "one of America's major ecologists" with a statement that her book belongs on the same shelf with Kerner's *Des Pflanzenleben der Donaulander*, Schroter's *Das Pflanzenleben der Alpen,* and Tansley's *Vegetation of the British Isles* (51, p. 10).

Although Victor Shelford, the first President of the ESA, was not a student of Cowles, he, too, was sufficiently influenced by him to be considered a part of his pedagogical genealogy. Shelford was apparently supportive of women in graduate education in these early days—he had three women PhDs in ecology between 1918 and 1927, one in 1938, and another in 1941. By contrast, his student Charles Kendeigh, who overlapped and succeeded him at the University of Illinois, had no women among his 51 PhD students. When the women PhDs who were Shelford's students sought jobs for which their degrees seemed to qualify them, however, they generally found their options limited to teaching in high schools or women's colleges, and in some of those colleges only if they remained unmarried. For example, Martha W Shackleford (PhD 1927) became a faculty member at Oklahoma College for Women; there is no evidence that she continued with research.

On the other hand, Shelford's student Minna Jewell (PhD 1918) taught at Kansas State Agricultural College (now Kansas State University) and Thornton Junior College, but in addition made significant experimental contributions to limnology during the Birge-Juday era at the University of Wisconsin when most research focused on surveys (10). Current researchers who specialize in various aspects of limnology have recognized Jewell's work as some of the first and most insightful on topics such as prairie streams (70), pH effects of fishes in acid lakes (74), groundwater-lake interactions (71), and freshwater sponges (72, 73) (T Frost, personal communication). Thus, she was a true pioneer in limnological research despite the barriers for women at this time. She published much of her work in ESA journals, i.e. *Ecology* and *Ecological Monographs,* and these articles are still cited in publications from 1986–1994

(Science Citation Index). Jewell did not have as many opportunities to have graduate students as Braun did, but apparently she "had quite an influence on young people" (10, p. 5). After Jewell retired from Thornton College, she taught in a girls' school in South America and continued to publish papers on freshwater sponges into the 1950s. Despite being a charter member of ESA and publishing significant data, Jewell did not receive recognition by either the Society or the limnological community during her lifetime.

In contrast to Lucy Braun and Minna Jewell, Mildred Faust and Harriet Barclay, two of Cowles's doctoral students, followed more traditional careers as gifted teachers. Mildred Faust obtained her PhD in 1933 and taught in the Botany Department at Syracuse University for her entire career, influencing many graduate students in their research; she was also active in conservation efforts and environmental education. Harriet George Barclay completed her doctorate in 1928 and married another University of Chicago botany graduate. The couple then went to the University of Tulsa where, unlike many married women of her time, Barclay had children but taught in the Botany Department alongside her husband from 1929 until her retirement in 1971. She concentrated much of her effort on carrying out the Cowlesian tradition of inspiring many undergraduate and graduate students through her infectious enthusiasm for field ecological studies of plants, not only at Tulsa University but at various field stations, particularly the Rocky Mountain Biological Laboratory. An alpine enthusiast, Barclay greatly increased the knowledge of Rocky Mountain and Andean plants through her extensive collections. The results of her continuous field research in Oklahoma were published mainly in the *Proceedings of the Oklahoma Academy of Science.* She was also an unstinting leader in conservation, for which she received numerous awards, particularly for her efforts in locating and preserving unique natural areas in Oklahoma, and she was elected to the Oklahoma Hall of Fame.

Women from Nontraditional Ecological Backgrounds

Several women not specifically trained as ecologists made significant research contributions that clearly fit within the framework of ecology. Emmeline Moore was an extraordinary woman who earned a PhD degree at Cornell in 1914. Immediately after obtaining her doctorate, she followed the pattern common among unmarried women of teaching at a women's college (Vassar). However, from 1917 to 1919 she worked on a US government project on primary food relations of fish, which led her into her future research career. She was the first woman given a permanent job in the New York State Conservation Department, where one of her first projects in 1920 was a collaborative survey of the biological, chemical, and physical aspects of Lake George. This study, which was set up by the New York State Legislature to determine how to increase fish productivity, was so successful that the biological survey was expanded to include the entire 60,000 square miles of the New York watershed (21). In 1926, Moore was appointed Director of the Biological Survey in the New York State Conservation Department. The original study and 16 subsequent reports published between 1926 and 1939 (all edited by Moore—112) remain the most comprehensive scientific examination of any state's water resources ever conducted (21); they emphasize her effective collaboration with other scientists. Although she did not teach during these years, Moore created a bond with numerous colleges and universities by hiring students and faculty for her summer field crews. This field training was significant in the development of careers of numerous biologists who would later become well known in their fields (21). Moore's work was recognized by another event unusual for a woman in 1927: election as the President of the American Fisheries Society.

Margaret Morse Nice was another outstanding pioneer who did insightful studies that can be considered ecological. She, like Edith Shreve, did not have a PhD. After receiving her baccalaureate from Mount Holyoke College, she entered Clark University for graduate studies. There she met and married Leonard Blaine Nice; soon after he obtained a doctorate, they moved to the University of Oklahoma where he became head of the Department of Physiology. She returned to Clark in 1915 to obtain her MA in zoology for research done earlier on the food of the Bobwhite. She later received honorary Doctorate of Science degrees from both Mount Holyoke and Elmira Colleges. Her first major publication, *The Birds of Oklahoma* (1925), was coauthored with her husband; her five children enthusiastically supported her field studies as well. In 1927 Nice's husband joined the faculty at Ohio State University. While in Ohio, Nice became a recognized ornithologist; during a very productive period from 1927 to 1936, she published for example, in 1933, a critical paper on territoriality (117). Her ideas regarding territoriality of birds were still heavily cited in 1980, 39 years after a 1941 paper (119) on the subject (R McIntosh, personal communication). It was her monographs on the life history of the Song Sparrow (e.g. 118, 120), however, that established her reputation as an outstanding ornithologist (180). She was elected President of the Wilson Ornithological Club (later Society) in 1938, becoming the first woman to serve as president of any major American ornithological society. In fact, throughout her later career she was highly praised by outstanding authorities, e.g. Tinbergen complimented her for "her cares and sacrifices in the home circle" and for service to science with "remarkable creative power." "Through your works you have become known to ornithologists throughout the entire world as the one who has laid the foundation for population studies now so zealously pursued" (180, p. 438). Ernst Mayer further stated, "I have always felt that she, almost single-handedly, initiated a new era in American ornithology and the only effective countermovement against the list chasing movements. . . . She was one of the first people in this country (? the first) to analyze a local deme. In other words, she pioneered left and right, as far as the US is concerned" (180, p. 438). Her devotion to research is indicated by the title of her posthumously published autobiography—*Research Is a Passion with Me.* A complete list of Nice's publications apparently does not exist, but the best estimates are that she published more than 250 titles on birds in journal articles, seven of book length, and 3313 reviews of the works of others. She continued her extraordinary activity through her long life (she lived to 90), but as she grew older she increasingly turned her attention toward educating the public about nature and conservation.

Nice wrote about the "tragedy" that women of intellect should have to spend so much time in manual labor. "Our highly educated gifted women have to be cooks, cleaning women and nursemaids . . . " (180, p. 433). However, in her case, Trautman (180) indicates that it would be difficult to overemphasize the important role her husband played in Nice's work, in encouraging her and providing the finances for conducting her researches and attendance at meetings. Nonetheless, Nice had to protest constantly that "I am not a housewife, but a trained zoologist," (14, p. 222). Konrad Lorenz wrote that "Margaret Morse Nice was the real founder of ethology" (14, p. 222). She rightfully received much recognition for her research, e.g. being elected to honorary membership in the British Ornithological Union and seven other ornithological or conservation societies. The fact that she never earned a PhD, was never a faculty member of a university, and received few or no grants and little secretarial assistance makes her achievements even more noteworthy.

Ecological Impact of a Woman Natural Science Writer

Even though Rachel Carson never proclaimed herself to be a professional ecologist, the ecological impact of her books makes it mandatory to include her in this historical discussion. She took both BA and MA degrees in zoology (the latter in part studying with Raymond Pearl at Johns Hopkins), but she was always interested in writing. She joined the Bureau of Fisheries (later the Fish and Wildlife Service) and was one of the first two women hired by this agency in other than clerical capacity. Known as a "well trained biologist with a gift for expression. . . " (20, p. 70), she moved rapidly from Assistant Aquatic Biologist in 1942 to Biologist and Chief Editor from 1949 until her resignation from the Service in 1952 to pursue writing full-time.

Although Carson's books *Under the Sea Wind* (1941), *The Sea Around Us* (1951), and *Edge of the Sea* (1956) were important contributions to natural history, it was *Silent Spring* (24), her last completed book, that had far-reaching ecological impact. Its publication came at a time (1962) when the concept of ecology was just becoming known to the public. *Silent Spring* was recognized within a decade of its publication as one of those rare books that "change the course of history... by altering the direction of man's thinking" (20, p. 227). Its success has been attributed to a combination of her biological background, her boldness in speaking her concerns, and her superb command of the English language. The book took a long time for her to write; ill with arthritis, cancer, ulcers, etc, she persisted in worldwide correspondence with countless experts (e.g. ecologists, ornithologists, physicians) because she said "long and thorough preparation is indispensable to do an effective job" (20, p. 243). She was deeply concerned about simplifying complicated technical data without introducing error. *Silent Spring*, serialized in *The New Yorker* in June, 1962 and published in its entirety in September, instantly created a sensation throughout the country.

The book was bitterly attacked, having initially offended the chemical and related industries as well as the powerful US Department of Agriculture. Continual attempts were made to discredit Carson as a "hysterical woman" (14, p. 271). Throughout the controversy, Carson's chief concern was that *Silent Spring* should have a lasting effect on government policy. Bitter reaction by many scientists to a negative report of the National Academy Committee on Pest Control and Wildlife Relationships led President Kennedy to ask for a study of the whole issue. A Pesticide Committee, set up by the Office of Science and Technology, in 1963 both criticized industry and agencies of the federal government and recognized the service performed by *Silent Spring*. The committee's report endorsed Carson's basic argument that insufficient scientific knowledge was available to assess accurately the risk of these toxic chemicals. By the spring of 1963 the book had become almost as famous in England as it was in America. *Silent Spring* was published during 1963 in France, Germany, Italy, Denmark, Sweden, Norway, Finland, and Holland and shortly afterward in Spain, Brazil, Japan, Iceland, Portugal, and Israel. In 1964, the last year of her life, honors were piled upon Rachel, e.g. Conservationist of the Year (National Wildlife Federation), Audubon Medal (the first to a woman), and American Geographical Society Medal. The most deeply satisfying recognition was her election to membership in the American Academy of Arts and Letters, which at the time had only three women members.

1935–1960 DEGREES: LATE PIONEERS

Much early ecological research was a loose amalgam of concepts, often "heavily influenced by taxonomic, habitat or geographical distribution of the organisms studied" (106). From 1935 to 1960, other avenues of ecological understanding appeared that are evident in women's research at that time.

Although a general downswing occurred in the percentage of women doctorates in ecology from the 1930s through the 1950s, several women who pursued degrees persisted in establishing successful careers, some becoming leaders in the field. It is notable, however, that Barbour (4), in an analysis of conceptual changes in vegetation studies during the 1950s, included only one professional woman ecologist (Langenheim) and two widows of prominent ecologists (Helen Buell and Linda Olswig-Whittaker) among the 34 persons interviewed for their opinions.

A Woman Leader in Aquatic Ecology

Although Ruth Patrick obtained her PhD in 1934 at the University of Virginia, Charlottesville, her prolific research record which spans much of the development of aquatic ecology, seems more appropriately discussed with the women in the late pioneer group. Occupant of the Frances Beyer Research Chair, Patrick Center for Environmental Research, Academy of Natural Sciences of Philadelphia, and Adjunct Professor at the University of Pennsylvania, Patrick has been an active researcher at the Academy since 1933. She apparently found a niche at the Academy and did not suffer the indignities that some women did in academia. She has used her background as a leading authority in the systematics of diatoms to do influential research in aquatic ecology. First, she pioneered the use of diatoms to infer paleoecological conditions (122). Her development of the diatometer permitted her to use a simple device to test important theoretical questions in ecology. For example, using glass slides of different sizes to simulate island size, she tested MacArthur and Wilson's theory of island biogeography. She demonstrated that the size of an area, available species pool and rate of invasion were the important components in defining the establishment and diversity of diatom communities, as had been shown for bird communities (123, 124). She further developed theories regarding the diversity and structure of river ecosystems (124, 126) and how shifts in these systems indicate that pollution is taking place before it becomes acute. Patrick developed the concept that a stream is an integrated community (125). She hypothesized that when pristine stream areas are equated by their structure and physical and chemical characteristics, they support similar numbers of species that remain relatively stable because the number of potential niches is similar. When pollution occurs, however, both numbers and kinds of species change significantly and the relative sizes of the populations become more variable than without pollution (125). Although she did not have a full academic appointment, well-known women researchers today in aquatic ecology and paleoecology mention her influence on the development of their thinking. She rightfully has been widely recognized for her work. For example, Patrick has been President of the Phycological Society of America and American Society of Naturalists, and she is a member of the National Academy of Sciences and of a staggering number of boards and committees. She has received countless awards, including the Tyler Environmental Award, and she was the first woman to receive the Eminent Ecologist Award, the highest award given by ESA to recognize research contributions. She has also received honorary doctorate degrees from 21 colleges and universities. After 62 years there, Patrick is still active in research at the Academy of Natural Sciences of Philadelphia.

A British Woman Pioneer

An Englishwoman, Verona Conway, with her PhD from Cambridge University in 1937, was a pioneer in blending field studies with application of experimental methods in physiological ecology (132). Her dissertation was designed to discover why an important bog sedge (*Cladium*) did not withstand annual cutting. She treated the annual wave of temperature through waterlogged peat quantitatively, predating the general application by ecologists of mathematical analysis to problems of environmental physics (132). She concluded that *Cladium* does not withstand annual cutting because the old leaves provide the pathway for oxygen to diffuse to the rhizome (37). Following appointment to a lectureship at the University of Sheffield, she investigated the ecology and origin of the blanket bogs of the Pennines, from which she critically analyzed dating and significance of recurrent surfaces in relation to current hypotheses of repeated climatic oscillations (39). She also wrote an influential monograph on the bogs of central Minnesota (38). Like many women ecologists, she was involved in conservation activities. In fact, she left her Sheffield lectureship in 1949 to join the newly formed British Nature Conservancy, where she analyzed the effects of burning and draining of peat surfaces on bog hydrology. Conway was recognized for her widely known studies by election to the Council of the British Ecological Society and later as an Honorary Member.

Cowles's Genealogy Revisited

Jane Claire Dirks-Edmunds was another of Victor Shelford's women PhD students (1941) at the University of Illinois. She expected difficulty in being accepted as a woman to do doctoral studies. However, when Victor Shelford was asked about Dirks-Edmunds, he answered, "Send me a good student, I don't care what sex they are" (121, p. 7)—indicating his attitude since the 1920s toward assisting women to obtain PhDs. For her dissertation, Jane compared part of the comprehensive information amassed on the Douglas fir–hemlock forest at Saddleback Mountain, Oregon [carried out by a Linfield College professor and his students (including her) from 1933 to 1938], with an analysis of the oak hickory forests of Illinois (49). She returned to Linfield College after obtaining her doctorate and initially was an assistant in the registrar's office. However, she was listed on the faculty roll as an instructor, partially because the American Association of University Women was beginning to use women faculty members with graduate credentials as one criterion for accrediting colleges (59). In 1946 she began to climb the professorial ladder slowly at Linfield, retiring as a full professor in 1974. She continued the Saddleback Mountain study, following the forest's succession subsequent to selective logging over 20 years, thus setting the framework for understanding future change in these forests. Pacific Northwest foresters have recognized the Saddleback Mountain research as "especially valuable" because it provides comprehensive data over a long period, initiated when little of this kind of ecological research was done on Pacific coast forests (121). Her devoted activities at Linfield College led to the establishment of the Jane Dirks-Edmunds Lecture there.

WS Cooper, one of Cowles' most prominent PhDs, had a number of doctoral students who subsequently sponsored women doctorates. For example, Catherine Keever and Elsie Quarterman completed their PhD degrees in 1949 with Cooper's student HJ Oosting at Duke University. They thought that opportunities opened to them to obtain doctorates because many men were away during World War II. Keever and Quarterman are appropriately presented together as they have done field work and have published together through the years. Keever taught in high school and several small colleges before obtaining her PhD, and afterward she settled as Professor of Biology at Millersville State College, Pennsylvania. Even with heavy teaching loads, she persisted with research, publishing on the causes of old-field succession and the distribution of major forest species in southeastern Pennsylvania (76). Characteristic of her positive professional attitudes, she has stated that, although there was little support for research at Millersville, she did not have the disadvantage of the publish or perish pressure (77). Thus she felt that she had the advantage of doing research because she wanted to, and she has continued to enjoy it since her retirement in 1974. The continuing impact of some of her perceptive successional studies are indicated by part of a title of a 1980 paper by McCormick and Platt "Catherine Keever—you were right!" (105).

Elsie Quarterman, Professor Emerita at Vanderbilt University, also initially taught in high school, but in 1943 she began her long tenure at Vanderbilt. Quarterman focused much of her research on the plant ecology of the Tennessee glade communities. To this end, she and her graduate students investigated the life history and community relationships of some characteristic glade species and endemics. Starting points were seed germination and life cycle studies, as well as interaction of species with physical factors of the environment and interrelationships of the plants with other biotic components, including allelopathic interference (139). Furthermore, with Catherine Keever she published a monographic study of the southern mixed hardwood forests (140), in which they described the pine-hardwood and immediate post pine stages in forest succession of the southeastern coastal plain, in an attempt to clarify existing ideas regarding climax there. The research of both Keever and Quarterman carries on the Cowlesian tradition of understanding the distribution of species in relation to their habitat, in defining successional status of communities and how this relates to possible equilibrium conditions. Quarterman supervised seven doctoral students, including Carol Baskin. Since her retirement, she actively continues conservation work, e.g. with The Nature Conservancy and as President of the Tennessee Environmental Council.

My own career (now as Professor Emerita of Biology, University of California, Santa Cruz) is part of the Cowles' lineage, as the only woman doctorate of WS Cooper (1953). I early followed the Cooperian tradition of doing research at the interface between ecology and geology, working together with my geologist husband in analyzing earthflow succession and vegetational patterns in relation to geology over a wide altitudinal range in western Colorado (e.g. 79). Nepotism regulations (1953–1961) allowed me only an honorary appointment as a Research Associate at the University of California, Berkeley and at the University of Illinois, Urbana. I too, therefore, taught part-time at women's colleges (Mills College and San Francisco College for Women). During this period my position was representative of numerous women scientists, and it underscores the important role of a few male ecologists whose sympathetic support helped circumvent nearly intractable administrative obstacles and thus enabled me to continue research. For example, I collaborated with HL Mason to use language analysis in provocative discussions of such ecological concepts as the environment and natural selection (e.g. 103). However, this kind of an unsupported research position often requires women to be versatile "research opportunists." This can be a deterrent in establishing their own research identity. On the other hand, for me it partially meant broadening my botanical background, which did prove useful later in my own research. Upon the independent pursuit of my own career, as a Research Fellow at Harvard University, I added the interface of chemistry to those of ecology and geology in investigating the paleoecology of amber (fossil resin), in ES Barghoorn's laboratory. The Radcliffe Institute for Independent Study (now Bunting Institute) played an important role in my obtaining the first professorial position for a woman in the sciences at the University of California, Santa Cruz (UCSC) in 1966.

At UCSC a major research interest evolved directly from my novel geochemically oriented paleoecological studies that opened new approaches to the study of amber. Contrary to traditional views, my survey of amber through 300 million years demonstrated the importance of angiosperm resin producers and that the greatest diversity of trees that produce copious amounts of resin occurred in the tropics (80). These results led me to direct my research toward the emerging paradigm regarding plant chemical mediation of some coevolutionary processes, in which I became a pioneer in tropical chemical ecology. My broad botanical background gave me the necessary scope to study in detail model tropical tree genera, which I carried out in collaboration with my graduate students and researchers in institutes in many Latin American and African countries (83). I experimentally analyzed environmental influences on the biosynthesis of terpenoids in both field and laboratory, and then assessed the role of the quantitative variation of these terpenoids in defense of both tropical and Pacific Coast plants against insects, slugs, vertebrates, and fungi. These long-term investigations resulted in an overall analysis of the phytocentric role of terpenoids, in which I challenged some currently held dogma in chemical ecology theory (82).

My years at UCSC further illustrate the trend toward an increasing number of graduate students supervised by women. I have supervised 36 graduate students (12 women) who have completed degrees (24 doctorates, of whom 8 have been women). I also coauthored a textbook, *Plant Biology in Relation to Human Affairs*, in which I emphasize an ecological perspective on the role plants play for humans. The breadth of my research resulted in my serving on numerous international and national committees. It also led to my election as the first woman President of the International Society of Chemical Ecology (1986–1987), as well as the second woman President of the Association for Tropical Biology (1985–1986), the Ecological Society of America (1986–1987), and the Society of Economic Botany (1993–1994).

Women Invade Plant Paleoecology

One of the dominant themes of dynamic ecology has been the long-term historical perspective of change in populations, communities, and environment. In fact, the development of Quaternary paleobotany closely paralleled that of ecology (188). The discovery by European researchers of well-preserved pollen grains in peat and sediments began the detailed and eventually quantitative analysis of post-Pleistocene vegetational and associated climatic change. Paleoecological studies, both Tertiary and Quaternary, initiated during the 1950s have provided important evidence in the revaluation of plant community concepts.

Three women who significantly contributed to the interrelationship between ecology and paleoecology received their degrees in the 1950s. Margaret Bryan Davis, Regents Professor in the Department of Ecology, Evolution and Behavior at the University of Minnesota, has a 1957 doctorate from Harvard University. Davis's ecological research interests have been at interfaces between ecology and geology, and between ecology and paleoecology. She is a long-time leader in the use of palynological data to study the organization of past communities and their dynamics, ecosystem processes, and response to climatic change. She was early influenced by Johannes Iverson, of the Danish Geological Survey, to use pollen for studying plant population and community dynamics in the recent geologic past. Hugh Raup, her Harvard graduate school mentor, perhaps further influenced her thinking with his skepticism regarding the concept of the organismal community and untested assumptions in general. Later, working with Edward Deevey at Yale, Davis demonstrated how accumulation rates in sediments are important in supplementing pollen percentages for inferring past population sizes (43). The first application of this approach (now standard palynological technique) at Roger's Lake, Connecticut not only helped to resolve the character of late-glacial tundra and boreal forest communities in New England, but showed that forest communities are loosely organized populations rather than a product of long evolutionary history units (44). This paper is the only one by a woman in the 1990 Collection of Classic Ecological Papers (147).

While at the University of Michigan, Davis compared pollen in surficial lake deposits with the composition of surrounding forests, which led to studies that she has pursued later in her career of lake circulation and deposition processes affecting the pollen content of the sediment. More recently, she is providing new empirical data regarding the stability of communities—with the fossil record typically demonstrating continuous community change and thereby challenging the concept of community equilibrium (45, 46). Her continued impact in introducing greater scientific rigor into Quaternary palynology via experimental and quantitative approaches, hypothesis testing, and model construction has led to a leadership role for fossil pollen analysis in current discussion of global environmental change (e.g. 47). Throughout her research Davis has guided numerous postdoctoral associates and graduate students. She has served on many national and international committees and advisory groups. Among her honors are election to presidency of the American Quaternary Association (1978), and the National Academy of Sciences (1982), and as a Fellow, American Academy of Arts and Sciences (1991). She was the third woman ESA President (1987–1988) as well as recipient of its Eminent Ecologist award (1993).

Davis points out that the enormous effort she had to expend struggling for opportunities came at the expense of science. As a woman she faced many problems in the process of becoming a professor with salary equivalent to that of men at the University of Michigan and Yale University, before going to the University of Minnesota as head of the department in 1976. However, she became visible in her efforts toward increasing the numbers and recognition of women in science. Her personal statements are poignant. "Now in my sixties, I find I have achieved the goal I was striving for all of my life. I am a professor in a department with a strong graduate program. I have a group of excellent students and my research combines ecology and paleoecology. In this benign environment I spend relatively little time on women's issues, but a decade or so ago I added up all the time I had spent, especially in my early years, maneuvering for laboratory space and for a faculty position, fighting for equal wages, taking on administration in order to improve my bargaining power, serving on committees on equity issues, mentoring women from undergraduates to full professors, and it comes to an appalling 25% of my total investment in science. My experience isn't unusual, either. In many ways I was advantaged by my education—many women have spent more energy than I maintaining their toehold on the academic ladder. Think how many women scientists there are in my generation and younger, all of us expending a quarter or more of our time and energy removing obstacles placed in our paths to slow us down. What a waste for human society that all that time and energy and talent didn't go into science instead" (MB Davis, personal communication).

Estella Leopold, Professor of Botany, University of Washington, was greatly influenced to become an ecologist by her father, the famous wildlife ecologist Aldo Leopold. After graduation from Yale (PhD 1955), Estella worked for the United States Geological Survey until 1976, using palynology to become a specialist in Tertiary history and development of western United States floras. Ruth Patrick was an important role model for her career as a young paleoecologist. Estella demonstrated in various fossil assemblages worldwide the principle that climatic forcing on Cenozoic time scales is a stimulus to evolution and extinction in plants (87). She showed that extinction and evolutionary rates of woody plants during the Late Tertiary were different from those of higher animals, i.e. while climate forced rapid changes in bursts, extinction rates over long periods were relatively slow for woody plants (87, 90). Significant studies of specific vegetation range from grasslands to Arctic tundra. For example, she demonstrated different timing and biogeographic origins for two grassland communities—the Great Plains from Miocene tropical ancestors and the Palouse from pan-Pacific boreal Pliocene ancestors (88). Her palynological studies from the Alaska Range show a warm temperate forest much like the mixed deciduous forest of eastern North America during the Miocene and Pliocene, which suggests surprising youth of tundra plant lineages and that deciduous forests occurred under photoperiod conditions unlike any in their present distributions (89). Leopold's research has been widely recognized; she was elected to the National Academy of Sciences (1974) and as President of the American Quaternary Association (1982). Furthermore, she has carried on her father's legacy of conservation activities, receiving awards such as Conservationist-of-the-Year from the Colorado Wildlife Federation, given jointly to Beatrice Willard (1969).

The third woman in this group is Grace Brush, Professor and Principal Research Scientist in the Department of Geography and Environmental Engineering at Johns Hopkins University, who took her PhD at Harvard University (1956). Her research opportunities varied as she moved to different institutions better suited to her husband's career than to her own. She had part-time appointments at four universities (George Washington, University of Iowa, Rutgers, and Princeton) before obtaining her present position at Johns Hopkins. She has persisted in doing research, however, with an approach alternating between modern and fossil plant distributions, which has served her well in bridging botany and geology. Her recent work has been influenced by the way many of her current engineering associates assess and approach problems. Some of her important contributions to ecology include 1) a vegetation map of Maryland, which shows the close relationship between lithologies that are similar hydrologically and distribution of natural forests (23), and 2) a reconstruction of estuarine history using a stratigraphic record that provides insights on human influence on the environment (22).

Wisconsin Women Plant Ecologists

Six women, supervised by John Curtis, received doctorates from 1953 to 1960 at the University of Wisconsin, Madison, near the time the large pedagogical genealogy of plant ecologists there began (111). They were also part of the re-evaluation of the plant community concept to which Curtis students contributed in the long-term detailed "continuum" analyses of Wisconsin vegetation, supporting the basic individualistic hypothesis of Henry Gleason. Three of these women, Margaret Gilbert (PhD 1953), Bonita Neiland (PhD 1954), and Gwendolyn Struik (PhD 1960), published their dissertations on various aspects of Wisconsin forest-prairie communities (60, 116, 176); then Gilbert became Professor at Florida Southern College, Neiland became Professor and Director of Instruction for the School of Agriculture and Land Management, University of Alaska, and Struik became a private consultant in New Zealand.

Another Wisconsin graduate, Martha Christensen, who was cosponsored by Curtis and mycologist Myron Backus (PhD 1960), not only published important studies on the role of soil microflora in various Wisconsin forests (27, 29) but continued research spanning mycology and ecology while she was a Professor of Botany at the University of Wyoming. She became a leader in the quantitative description of soil microfungal communities. She ordinated microfungal communities and correlated patterns of other biotic and abiotic factors against the patterns dictated by the fungi, thus demonstrating, against commonly held ideas, the existence of habitat specificity for soil microfungi, particularly in forest ecosystems (28). Christensen's numerous achievements in studying the ecology of soil fungi led to her election as the third woman President of the Mycological Society of America (1985–1986).

A Woman Desert Ecologist

Janice C Beatley earned her 1953 PhD at Ohio State University. She taught at several small colleges before becoming a research ecologist at the Laboratory of Nuclear Medicine and Radiation Biology, University of California, Los Angeles (1960–1972). Beatley wrote notable papers on desert community dynamics at the Nevada Test Site with a focus on reproduction of annual plants (8); she also investigated the dependence of rodents on these annuals (9). Her research on the ecological status of introduced brome grasses (7) was one of the first contributions regarding the invasive nature and ecological significance of these annual grasses. Her highly respected research is still used in teaching (B Strain, personal communication). From 1973 until her death in 1987, Beatley was a professor at the University of Cincinnati, where she fulfilled a long-time dream of teaching in the same department where E Lucy Braun had maintained her lifetime affiliation. Here Beatley directed her research toward understanding the wintergreen herbaceous flora of deciduous forests.

Women Animal Ecologists

Margaret Stewart and Frieda Taub are 1950s graduates who have done research in areas of ecology different from those of most contemporaneous women. Margaret Stewart, Professor of Biology, State University of New York, Albany (Cornell PhD 1956), has carried out field studies of behavior and population and community ecology of amphibians in both temperate and tropical ecosystems. She is one of the relatively few women ESA members even today doing active research in animal behavior (181). Her book *Amphibians of Malawi* in 1967 established her reputation in herpetology (172), and she was the first person to spearhead ecological and behavioral studies of the tropical terrestrial frogs (*Eleutherodactylus*), which are major vertebrates in the Antilles. Her work demonstrating that retreat sites, rather than food, are a major factor in population regulation of tropical forest frogs gained wide attention (174); recently she completed a summary of 15 years of fluctuation in a deme of frogs in Puerto Rico rainforests in relation to climate, which has important implications in the assessment of declining amphibian populations (173). Stewart's leadership role in her field has been recognized by her recent election as President of the American Society of Ichthyologists and Herpetologists and by the honorary doctorate she received from the University of Puerto Rico, Mayaguez. She, too, is actively engaged in various conservation projects locally and internationally.

With a zoology doctorate in 1959 from Rutgers, Frieda Taub went immediately to Seattle because her husband took employment there. She stated, "as a result of my inexperience as well as suspicion of women having a PhD in 1959, . . . I had to begin at an entry level research position in the College of Fisheries at the University of Washington" (F Taub, personal communication). However, by 1971 she had risen to full professor in the College. She used the concept of microcosms as a tool in analyzing ecological interactions in the regulatory process of releasing new chemicals into the environment (177). She removed a major objection to use of complex communities in testing ecotoxicological responses with a summary of evidence that microcosms allow validation of these tests among laboratories (179). Taub's leadership role in the IBP Coniferous Biome project led to her edited book, *Lakes and Reservoirs* (178), a volume in *Ecosystems of the World,* which takes a comparative approach in emphasizing the similarities of processes underlying the uniqueness of each ecosystem.

1961–1975 DEGREES: FIRST "MODERN" WAVE

Following the coincidence of the environmental and women's movements in the 1960s, there was an increase in number of women ecologists, the institutions from which they obtained doctorates, and the positions they were able to obtain in major universities, where greater opportunity for research existed (Table 1).

A Woman Mathematical Ecologist

The research of EC Pielou represents the emergence of a woman working in an area that continues to be dominated by men. In fact, she has a novel professional history that displays an amazing sense of self-motivation. Pielou was equally interested in natural history and mathematics, and while caring for young children with the help and support of her husband, she did research in mathematical ecology as an amateur. She has written that "as an amateur I was beholden to nobody and could follow my inclinations and make my own decisions without the need to justify them to granting agencies, senior academics, or anybody else. . . " (EC Pielou, personal communication). In 1962, with no supervisor or committee, she was able to convert several published papers into a PhD from the University of London. She spent four years as a Research Scientist in the Canadian government, then entered academia as a full professor, first at Dalhousie University, Nova Scotia, and then at University of Lethbridge, Alberta. Again in her own words, "Starting at the top has its obvious advantages. I have been my own boss all of my working life. . . " (EC Pielou, personal communication). Throughout her research that has spanned boreal forests to intertidal marine algae, her aim has been to postulate ecological hypotheses in clear, mathematical form and to design rigorous tests specific for each hypothesis.

Pielou has written six books. Her *Introduction to Mathematical Ecology* (127) and its expanded second edition (131) have had great impact. She also has written *Population and Community Ecology* (1974), *Ecological Diversity* (1975), and *Interpretation of Ecological Diversity* (1984). In journal articles she has developed a mathematical measure of closeness of association among a group of several species, which serves as a measure of the "structure" of many-species communities (128). She extended the application of Leslie matrices to populations of two competing species of sessile organisms in a study of how the interactions between populations affect their spatial patterns (129). She has been equally interested in interrelationships among ecology, biogeography, and their paleo equivalents. Because a mathematical approach to problems in biogeography lagged far behind that in ecology, she analyzed the statistics of biogeographic range maps (130).

Since retiring in 1988, Pielou has written three books for general readers, bridging the gap between research ecologists and interested amateurs who do substantial work on environmental protection. These books put into easily comprehensible form ecology of the world's northern evergreen forests, the return of life to glaciated North America after the Ice Age, and a naturalist's guide to the Arctic. She was given the Lawson Medal of the Canadian Biological Association and was the second woman to receive the Eminent Ecologist Award from ESA (1986).

Cowles' Genealogy Continued: Expansion into Wider Activities

Although the six women within the Cowles lineage in the First Modern Wave (1961–1975) were oriented toward some phase of plant ecological research for their degrees, the careers of four of them tended toward applied research.

Nellie Stark, another Oosting PhD (1962), now Professor Emerita of Forest Ecology, University of Montana, Missoula, was a pioneer, becoming a full professor in a US forestry school in 1979. She had worked for the US Forest Service in the Sierra Nevada Mountains and the Desert Research Institute in Nevada before going to Montana. Stark developed thought-provoking concepts, such as direct nutrient cycling for tropical rain forests on nutrient-depleted soils. This led her to the concept of "biological life of a soil" (170), which she further applied in evaluation of nutrient losses from Rocky Mountain forests in terms of long-term productivity (171). Other studies included the impacts of logging and fire on conifer forests and the resistance and resilience of forest ecosystems to chemical perturbation such as acid rain.

Beatrice A Willard took her PhD in 1963, supervised by Cowles' descendent John Marr, at the University of Colorado. She taught briefly in colleges before answering the call of applied ecology, initiated by the passage of environmental legislation in the 1960s. Willard became Executive Director and then

Table 1 Women discussed 1900–1976, date and university of PhD, area of ecology when degree was taken and later if changed, and primary institution where research was done (M—has been married; C—has children; aC—unmarried, has adopted child; * no complete information regarding family)

Name	Year (PhD)	University	Area of ecology	Current or major institution after degree
Early Pioneers				
Edith S Clements (M)	1904	Nebraska	Plant Ecology	None
Edith B Shreve (M-C)	1902 (BA)	Chicago	Plant physiological ecology	CIW
E. Lucy Braun	1914	Cincinnati	Plant ecology	U. Cincinnati
Emmeline Moore	1914	Cornell	Limnology	New York State Conservation Dept.
Margaret Nice (M-C)	1915 (MA)	Clark	Avian population studies	None
Frances Louise Long	1917	Minnesota	Plant ecology	CIW
Minna Jewell	1918	Illinois-Urbana	Aquatic ecology	Thornton College
Martha Shackleford*	1927	Illinois-Urbana	Community ecology	Okla. College for Women
Harriet G. Barclay (M-C)	1928	Chicago	Plant ecology	U. Tulsa
Mildred Faust	1933	Chicago	Plant ecology	Syracuse U.
Rachel Carson (aC)	1932 (MA)	Johns Hopkins	Natural history, conservation	U.S. Fish & Wildlife Service
Late Pioneers				
Ruth Patrick (M-C)	1934	Virginia	Aquatic ecology	Acad. Nat. Sci. Philadelphia
Verona Conway	1937	Cambridge	Plant physiological ecology	Sheffield U.
Jane C. Dirks-Edmunds	1941	Illinois-Urbana	Community ecology	Linfield College
Elsie Quarterman	1949	Duke	Plant ecology	Vanderbilt U.
Janice Beatley	1953	Ohio State	Plant ecology	UC Los Angeles NM & RB; U. Cincinnati
Catherine Keever	1949	Duke	Plant community ecology	Millersville State College, PA
Jean Langenheim (M)	1953	Minnesota	Plant community & chemical ecology	UC Santa Cruz
Margaret Gilbert	1953	Wisconsin-Madison	Plant community ecology	Florida So. College
Estella Leopold	1955	Yale	Plant paleoecology	U. Washington
Margaret Stewart (M)	1956	Cornell	Animal behavioral ecology	SUNY Albany
Bonita Neiland (M*)	1956	Wisconsin-Madison	Plant community ecology	U. Alaska
Grace Brush (M-C)	1956	Harvard	Plant paleoecology	Johns Hopkins U.
Margaret Davis (M)	1957	Harvard	Plant paleoecology	U. Minnesota
Frieda Taub (M-C)	1959	Rutgers	Microcosm ecology	U. Washington
Gwendolyn Struick (M*)	1960	Wisconsin-Madison	Plant community ecology	Private consultant
Martha Christensen	1960	Wisconsin-Madison	Forest soil fungal ecology	U. Wyoming

Table 1 Continued

Name	Year (PhD)	University	Area of ecology	Current or major institution after degree
First Modern Wave				
E.C. Pielou (M-C)	1962	London	Mathematical ecology	Dalhousie U. & U. of Lethbridge
Nellie Stark (M)	1962	Duke	Plant physiological ecology; forestry	U. Montana
Betty Willard	1963	Colorado	Plant ecology; conservation	Colorado School of Mines
Mary Willson (M)	1964	Washington	Avian and forest ecology	U. Illinois; U.S. Forest Service
Deborah Dexier	1967	North Carolina-Chapel Hill	Marine ecology	San Diego State U.
Carol Baskin (M)	1968	Vanderbilt	Plant ecology	U. Kentucky
Joy Zedler (M-C)	1968	Wisconsin-Madison	Plant & wetland ecology	San Diego State U.
Rebecca Sharitz (M)	1970	North Carolina-Chapel Hill	Plant population & wetland ecology	U. Georgia-Savannah Labs
Frances James (M-C)	1970	Arkansas	Avian ecology	Florida State U.
Judith Myers (M-C)	1970	Indiana	Animal population ecology	British Columbia U.
Katherine Ewel (M)	1970	Florida, Gainesville	Forest-wetland (systems) ecology	U. Florida-Gainesville
Maxine Watson (C)	1970	Yale	Plant population ecology	Indiana U.
Nancy Slack (M-C)	1971	SUNY Albany	Plant & bryophyte ecology	Russell Sage College
Berly Robichaud Collins (M)	1971	Rutgers	Plant ecology; conservation	McGraw-Hill Information Services
Patrice Morrow	1971	Stanford	Plant physiological ecology → plant-insect interaction	U. Minnesota
Sarah Woodin (M-C)	1972	Washington	Marine ecology	U. South Carolina
Pat Werner (M)	1972	Michigan State	Plant population ecology	U. Florida-Gainesville
Barbara Bentley (M-C)	1973	Kansas	Plant-insect interaction	SUNY Stony Brook
Beverly Rathcke (M)	1973	Illinois, Urbana	Insect-plant ecology	U. Michigan
Laurel Fox (M-C)	1973	UC Santa Barbara	Insect-plant interaction; community ecology	UC Santa Cruz
Susan Martin	1973	UC Santa Cruz	Plant (crop) chemical ecology	USDA; Colorado State U.
Karen Porter (M-C)	1973	Yale	Aquatic ecology	U. Georgia
Susan Riechert (M-C)	1973	Wisconsin-Madison	Spider behavioral ecology	U. Tenn.-Knoxville
Frances Chew (M)	1974	Yale	Insect-plant ecology	Tufts U.
Martha Crump (M-C)	1974	Kansas	Animal behavioral ecology	U. Florida-Gainesville
Judy Stamp	1974	UC Berkeley	Animal ecology	UC Davis
Jane Lubchenco (M-C)	1975	Harvard	Marine ecology	Oregon State U.
Deborth Rabinowitz (M)	1975	Chicago	Plant population ecology	Cornell U.

President of Thorne Ecological Institute in Boulder, Colorado (1965–1972), where she built bridges by interpreting ecology and its utility to non-ecologists. She had an important overview role on the effects of the Alaska pipeline while on the Council of Environmental Quality in the Executive Office of the President. Subsequently, she established and became the head of the Department of Environmental Sciences and Engineering Ecology at the Colorado School of Mines. As Director, Industrial Ecology Institute, she formed a bridge between ecology and the mining industry. Despite her administrative duties, she continued to publish significant scientific articles about the impact of human activities on the Rocky Mountain tundra (e.g. 189). Willard has received an impressive number of awards for her environmental work, ranging from engineering institutes (Environmental Conservation Distinguished Service Award—1979) to the US Forest Service (75th Anniversary Award for promoting ecological awareness and understanding—1980) to the United Nations (Outstanding Environmental Leadership Award—1982).

Carol Baskin, a 1968 PhD with Elsie Quarterman, went directly from Vanderbilt to the University of Kentucky as the wife and research partner of Jerry Baskin, who was also a PhD student of Elsie Quarterman. The Baskins are well known for their prolific publication (230 articles as of 1994) on topics such as autecology of endemic limestone glade plants, ecological life histories, and seed germination studies of herbaceous plants, inspired initially when they were students of Quarterman. The Baskins represent an outstanding example of close and continuous family partnership in research. However, despite very high research productivity, Carol had no official appointment at the University of Kentucky until 1984, when she was made an Adjunct Professor in the School of Biological Sciences. Among her many publications, recent autecological syntheses have been of particular interest, e.g. a joint article with her husband (6) in which they first synthesized dormancy cycles of seeds. They point out the way seeds of summer vs winter annuals respond to seasonal temperature, and for the first time they applied the term "continuum" to gradual changes that occur in a seed's physiology as it goes in and out of dormancy. Another synthesis includes many of their individual publications, bringing together information on the germination phenology of 274 herbaceous species in temperate climates and dormancy break and germination for 179 of them. They organized the data by type of life cycle and discussed them with regard to phylogenetic relationships (5). The Baskins' systematic long-term study of a specific aspect of autecology now enables them to reach broad generalizations. Carol has been recognized by election as Secretary of the Botanical Society of America (1980–1984).

Beryl Robichaud Collins has had an unusual career, which displays her persistence in using research to have an impact on conservation. Her undergraduate major was in economics, and she was fully employed in information services (Senior Vice President, McGraw Hill) when she took her PhD with Murray Buell at Rutgers in 1971. Pursuing graduate work on a part-time basis was not the usual practice, but she was highly motivated to obtain a strong scientific background to contribute effectively to public decision-making in environmental affairs. She co-authored *Vegetation of New Jersey: A Study in Landscape Diversity* (152) and recently co-edited the volume *Protecting the New Jersey Pinelands: A New Direction in Land-Use Management* (36). She serves on the Board of Governors of The Nature Conservancy and has received two honorary doctorates for her achievements.

Susan S Martin (PhD 1973) at UCSC also turned toward applied ecology in taking a position with the US Department of Agriculture's Agricultural Research Service (ARS) in Fort Collins, Colorado and as a Faculty Affiliate in the Biology Department, Colorado State University. She applied the chemical ecological approach she had used in her graduate work with Langenheim on resin chemistry of tropical legumes to studies of chemical mediation of plant-pathogen interactions in crop plants such as sugar beet (101). Martin has also been concerned that studies of stress-related compounds in crop plants often have ignored the potential variability that may arise from genetic variation or environmental influence. As a result, she investigated environmental influences and the role of ecotypic differentiation of diverse populations in analysis of phytoalexin accumulation in a common forage legume (102). Also, she is deeply involved with plant conservation in Colorado.

Patrice Morrow, Professor and Head of the Department of Ecology, Evolution and Behavior at the University of Minnesota, took her PhD (1971) in plant physiological ecology with Dwight Billings' student Harold Mooney at Stanford University. In California, Morrow was concerned with effects of drought on plant productivity; however, while a Fulbright postdoctoral fellow in Australia, she became impressed with the effects of insects that consume a large proportion of the photosynthetic surface of *Eucalyptus*. In fact, she became convinced that insect damage was a much greater problem for eucalypts there than adjustment of photosynthesis to seasonal temperature changes. Morrow since has used eucalypts to test aspects of plant defense theory that would be difficult to test where insect effects on plant growth are apparently minor. In her early work on eucalypt tree rings, she demonstrated that insect attack was chronically heavy and suggested that this kind of damage had been rampant in Australia for a long time (114). She pursued this perspective later with comparative estimates of presettlement insect damage in Australian and North American forests, in which higher damage levels were consistently found in Australia (113). This research was part of long collaboration with Laurel

Fox on Australian eucalypts. Although they have had independent research projects, in their joint efforts Fox's perspective in insect population biology complemented that of Morrow's in plant ecophysiology. Another influential paper grew out of their discussions regarding how communities are structured and problems associated with concepts of insect specialization, i.e. whether it was a species property or local phenomenon (58). Morrow has been recognized in ESA by election as a Council member (1986–1988) and as Vice President (1993–1994).

Prominence of Women in Emerging Study of Interactions of Insects and Plants

Morrow's research shift from traditional plant physiological ecology to interactions of insects and plants is representative of the beginnings of an emphasis in this area by a group of women. McIntosh (107, p. 44) refers to this subfield "as a 'growth industry' of ecology . . . used extensively in discussion and tests for ecological theory."

The very productive collaboration of Laurel Fox, Professor of Biology, University of California, Santa Cruz, and Morrow is somewhat similar to that between two other women ecologists, Catherine Keever and Elsie Quarterman. Fox earned her PhD at UC Santa Barbara in 1973 with Bill Murdock and Joe Connell, working on predation of generalized stream insects. She spent several years as a postdoctoral and research fellow at the Australian National University where she switched to research on herbivory, not only because of the large, obvious herbivore damage on eucalypts, but because she wanted to test theoretical assumptions regarding specialist insects. Since 1978 she has split a professorial appointment at UCSC in the Biology Department with her ecologist husband; both Fox and Morrow were able to continue research in Australia after they took their US professorships. Fox has challenged some conventional ideas about insect-plant interactions as this area of research has developed. For example, she and Macauley (57) were the first to show that tannins, although abundant in eucalypts, were not an insurmountable defense for at least some insects, and they suggested that gut pH might be part of the reason. They also demonstrated the crucial importance of leaf nitrogen for insects consuming leaves with such low nitrogen levels as eucalypts. This publication became a citation classic and was significant in leading to current advances in thinking about the roles of tannins. She challenged two major ideas about ecology and evolution of insect-plant systems: 1) aspects of apparency and its assumptions about the cost of defense, and 2) pair-wise co-evolution might not be the appropriate model for systems in which large numbers of herbivores feed on the same plants (56). Fox & Morrow (58) argued that researchers used the concept of specialization very loosely—herbivorous insects that might use one or a limited number of plant species in one place might feed on other plants elsewhere. They presented ecological and evolutionary reasons why the diets might be restricted, which led to studies by numerous ecologists that show genetic differentiation among insect populations to food plants (58).

The research of Judith Myers, Professor of Zoology, University of British Columbia (PhD 1970, Indiana University), spans several areas in ecology but has recently emphasized insect-plant interactions. Two themes recur throughout Myers' research: experimental ecology and critiques of overly simplified generalizations (adaptive sex ratios, genetically structured populations, and induced defenses). Her PhD research on voles ultimately led to a review with CJ Krebs, which became a citation classic (78). This work included early hints to later findings that behavior of females should not be overlooked in population studies. Meyers acknowledges the important assistance from a postdoctoral fellow, Kathy Williams, through the hectic years of having two small children. Myers and Williams analyzed the highly popular and oversimplified view that induced chemical defenses control population dynamics of forest caterpillars (190). Recently Myers (115) reviewed her continued significant research on tent caterpillars.

Barbara L Bentley, Professor of Ecology and Evolution at SUNY Stonybrook, is another of the relatively large 1973 crop of PhDs—in her case from the University of Kansas (Table 1). She quickly saw the value of the emerging style of field research that involves manipulation of a natural system, with her dissertation concerning the interhabitat differences of plants bearing extrafloral nectaries and the associated ant community in reduction of herbivore damage (11). Her research has continued to be characterized by field experimentation. In her research on epiphylls, she was the first to bring high technology (gas chromatography) to the Costa Rican rainforest (12), demonstrating how field ecologists could thus greatly expand the range of questions they were asking. Recently, she was among the first to look at effects of elevated CO_2 on plant-insect interactions, particularly including nitrogen fixation and multilevel interactions (13). Part of her goal in these studies has been to develop information pertinent to policy decisions regarding global change. Bentley has been involved with environmental policy in the development of the Decision Makers' Course, when she was Vice President for Education in OTS. She was also elected Vice President of ESA (1989–1990). Bentley's successful career has been accompanied by rearing children; although she admits they have interfered somewhat with her career, she thinks that serving as a good role model in her department has allowed students (and fellow female faculty) to have children in a "much more neutral environment" (B Bentley, personal communication).

A 1973 PhD from the University of Illinois, Beverly Rathcke is Professor of Biology, University of Michigan. Always interested in insects as a child, “her career was settled when she discovered in college that she could study insects and plants for a living” (B Rathcke, personal communication). After obtaining an MS degree at Imperial College, London University, she started her doctorate at Cornell; however, marriage took her to the University of Illinois, where Mary Willson was a female role model. From 1975 to 1978 she had an unsalaried research title at Brown University where her husband taught. Rathcke then accepted an Assistant Professorship at the University of Michigan. Her research on a guild of stem-boring insects contradicted the major predictions from competition theory at a time when it was not popular to do so (144). In this and later studies of flowering phenologies she used random models, which were important because they allowed for testing specific hypotheses and resulted in rejection of then-current dogma generated from competition theory (145, 146). These contradictory results promoted re-evaluation of earlier evidence, the design of more rigorous tests of competition, and the consideration of alternative hypotheses, including facilitation or the positive interactions among species.

Another woman who pioneered research on the interactions of insects and plants with some emphasis on chemical mediation, Frances Chew, Professor of Biology at Tufts University, has a Yale PhD (1974). As a postdoctoral fellow at Stanford, she was intrigued by the concept of coevolution of plants and insects mediated by plant secondary chemistry, then being proposed by Paul Ehrlich and Peter Raven. Chew’s research became motivated by the single overarching question of what determines insect-host plant specificity; most of her work has been on *Pieris* butterflies and their host plants (the Cruciferae and allies). With JE Rodman, she was the first to show a “community profile” of plant chemistry (153). She utilized concepts in plant population biology and plant apparency in studies assessing the evolutionary escape from herbivory (25), and she showed that differential host utilization by closely related insect species is mediated by differential sensitivity to plant chemistry (26). Chew’s special research contribution has been to establish a strong tie between natural history of a system and critical laboratory work analyzing its parts.

Women Studying Avian Ecology

Studies of birds have always been important in shaping ecological theory (106) and, following the early lead of Margaret Nice, women have added their part.

A 1964 PhD, working with Gordon Orians at the University of Washington, Mary Willson has been a prolific researcher of unusual versatility in ecological and evolutionary studies of plants and animals. Her dissertation, which focused on mating systems in birds, was one of the first studies showing ecological correlates of harem size, and thus it opened the door for the first-generation mating system models with Yellow-headed Blackbirds (191). She was an instructor at Simmons College before going to the University of Illinois where she progressed to full professor in 1976. There she inspired many graduate students and began her studies of plant reproduction, making a controversial suggestion that sexual selection occurs in plants (192); later she compared sexual selection in plants and animals. She also studied the relationship between avian frugivory and seed dispersal (193). During this time she produced two books, one on plant reproductive biology and the other on vertebrate natural history. Although Willson contributed richly to research while at the University of Illinois, in 1989 she opted for the strictly research position of Research Ecologist at the Forest Science Laboratory, Juneau, Alaska. Here she has continued to expand her research horizons to include seed dispersal spectra in comparing plant communities (194), evolution of fruit color in fleshy-fruited plants (195), association of mites and leaf domatia, and endemic birds in fragmented south-temperate rainforests in Chile.

Professor of Biology at Florida State University, Frances James is a 1970 PhD from the University of Arkansas, where she began research on intraspecific size variation in birds and tight negative correlations with environmental variables that are functions of temperature and humidity (66). A simultaneous project on habitat relationships of birds, based on a Gleasonian approach and expressed as multispecies habitat relationships along multivariate axes, introduced the concept "niche gestalt," which won her the Edwards Prize from the Wilson Ornithological Society (67). Subsequent approaches, expanding ideas from her dissertation research, have included cross-fostering experiments with Red-winged Blackbirds (68). Her efforts to standardize sampling procedures and to quantify geographic variation in habitat at the intraspecific level led to an evaluation of applications of multivariate analysis in ecology and systematics (69). James has served in leadership roles on many committees and boards, and was elected a Council member of ESA (1977). She has made her mark in ornithological societies by being the first woman President of the American Ornithologists' Union (1984–1986) and receiving its Elliott Coues Award (1992), given for contributions that had impact on bird research in the western hemisphere.

Women Aquatic and Wetland Researchers

Joy Zedler, Professor of Biology and Director of the Pacific Estuarine Laboratory, San Diego State University, has a professional history reflecting problems that married women have often faced early in their careers, although the difficulties have tended to improve over time. While a graduate student in plant ecology with Orie Loucks at the University of Wisconsin, Madison, she married another ecologist; after her PhD (1968), she and her husband went to the University of Missouri and then to San Diego State University. Zedler took various low-paying jobs until finally she obtained a tenure-track position at San Diego State; her promotion to tenure, however, was delayed because she took time off to have children. Her research has been important in changing ideas about coastal wetlands. Her suggestion that algae under the marsh canopy could be as productive as vascular plants, where high salinity apparently selects for shorter open canopies, was foreign to researchers of the Spartina marshes of the Atlantic and Gulf of Mexico coasts, where most US salt marsh studies have been done (199). Thus, she changed the prevailing dogma that vascular plants are always the base of the estuarine food web and highlighted the importance of epibenthic microalgae. One of the themes in Zedler's career has been to take science into the management arena. Her series of studies on restored and natural wetlands in San Diego Bay have demonstrated the problems with attempts to recreate habitats of endangered species (200). She has worked with the National Research Council on aquatic ecosystem restoration and on its current wetland delineation book; she is also on the governing board of The Nature Conservancy.

Katherine Ewel, Professor of Systems Ecology in the Department of Forestry, University of Florida, Gainesville, also had to adapt to jobs according to where her husband was located. Receiving her degree in vertebrate zoology (PhD 1970, University of Florida), Ewel spent two years as an Instructor at Duke University while her husband finished his PhD at the University of North Carolina. At Duke she became skilled in the use of physical and computer models in biology. Although there were no job prospects for her at the University of Florida where her husband accepted a job, she was fortunate to have colleagues encourage collaboration based on her newly developed talents in computer modeling. After considerable research as a systems ecologist at the University of Florida's Center for Wetlands, she successfully competed for an assistant professorship in the School of Forest Resources and Conservation Engineering Sciences, becoming the first woman to hold a tenure-track position in that unit. Ewel has made two kinds of contributions to ecology. First, she has brought attention to the importance of different kinds of wetlands, demonstrating interrelationships among the different values that society places on these wetlands and compromises a manager must make in choosing among them (52). She has proposed a relationship between productivity and hydrology that establishes a framework for distinguishing quantitatively among different kinds of wetlands within a region (53). Secondly, she synthesized decades of field research together with current understanding of the magnitude and interaction of material flow to propose carbon, water, and nutrient budgets and their interrelationships for a major forest type in the southeastern United States (54).

Nancy Slack, Professor of Biology at Russell Sage College, earned a PhD in ecology following two Cornell degrees, although her degree was somewhat delayed (1971 SUNY Albany) because of marriage and family. Slack has had a career based on highly motivated interest and persistence. She became fascinated with the ecology of bryophytes, a group often ignored, and she adapted ordination methods for use with bryophytes in determining species diversity and community structure (including both vascular plants and bryophytes) along an elevation gradient in the Adirondack Mountains (162). In collaboration with DH Vitt, Slack worked on minerotropically rich fens in Alberta (165). They also discovered that Sphagnum species are remarkable ecological indicators, and they did the first quantitative American bog study including Sphagnum and initial work on niche theory of bryophytes. Slack then developed in depth the concept of niche for bryophytes (163). Thus, despite teaching at a college that does not have graduate students in biology, she has persevered in seeking out collaborators with whom she could expand her research. Best known as a peatland ecologist, she has studied boreal mires from New York to Minnesota, Alberta, British Columbia, and Sweden. She has long been involved in conservation work, serving as a board member and land evaluator for The Nature Conservancy. She also has written two semipopular books on alpine ecology.

Karen Porter, Professor of Zoology in the Institute of Ecology at the University of Georgia, has been fortunate in the opportunities to manage her career and marriage. She and her husband obtained their PhDs from Yale University in 1973 and went immediately to tenure-track positions at the University of Michigan. The good fortune to have two positions enabled them to be professionally independent from the beginning. When they moved to the University of Georgia as Associate Professors, she was a part-time faculty member while she had a daughter, but two years later was returned to full-time. Her research has been focused on aquatic ecology, particularly lake plankton, which has been an expansion of her childhood love of lakes and the sea. She is one of the few women graduate students of Hutchinson. Like Estella Leopold, Porter acknowledges the role of Ruth Patrick during her graduate studies. Although she had early done laboratory studies, e.g. adapting a fluorescent stain for counting free-living bacteria, allergies to laboratory chemicals led her to emphasize field studies, some of which she has done collaboratively with her husband. Some of her most important papers have been syntheses; in fact, one of her first papers was a synthesis of ideas (hers and others) on the potential role of filter-feeding zooplankton in controlling phytoplankton community structure, succession, and co-evolution (133). A second one, evolving from 50 papers done in collaboration with a number of PhD students, is on the microbial-based planktonic food web of Lake Oglethorpe, Georgia, in which she has integrated the microbial loop and classic food chain into a realistic planktonic food web (134). This is one of the first studies to show the effect of microbial production on higher trophic levels based on consumers such as flagellates, rotifers, and larval fish. Since northern lakes are warming, there is considerable interest in a third synthesis, encompassing Porter's 17 years of field data on warm temperate Lake Oglethorpe and the limnology of southwestern monomictic lakes in relation to climate change (135). Porter's first authored research in the 1990s has received 60–190 citations per year, particularly noteworthy in that the study of planktonic food webs does not constitute a large subfield of ecology; her creativity has been recognized by her receiving the University of Georgia Creative Research Medal.

Importance of Women as Plant Population Researchers

Whatever the reasons, studies of plant population dynamics lagged behind human demography and theoretical and experimental studies of animals (106). Terrestrial plant ecologists in the first half of the twentieth century spent much of their effort describing, classifying, and mapping communities. But in the 1970s, plant population biology went through a "revolution"; in fact, Antonovics (3) thought it to be one of the most important events in ecology at the time. It is a paradigm change in which women were early participants, and an aspect of ecology in which they still are prominent (181).

A 1970 PhD from the University of North Carolina, Rebecca Sharitz is one of the pioneer women plant population ecologists. Currently Senior Ecologist at the Savannah River Ecology Laboratory and Professor in the Department of Botany, University of Georgia, her research includes the population dynamics of plants in swamp forest systems and responses of these communities to environmental disturbance. Sharitz early demonstrated experimentally the role of competition in structuring plant communities across a resource gradient, and she presented one of the first examples of using life table techniques in the analysis of plant populations demography as well as relay floristics in primary succession (156). Another important contribution is an eight-year collaborative study that provided rigorous analysis of temporal and spatial patterns of natural seedling recruitment of woody species in bottomland hardwood forests (75). Recently, she suggested ways in which ecological concepts can be brought into management of southern forest resources (155). She was one of the first women elected an ESA Council member (1975); she was Treasurer (1987–1990) and Vice President (1990–1991); and currently she is Secretary General of the International Society of Ecology (INTECOL).

One of the women doctorates supervised by G Evelyn Hutchinson (Yale 1970), Maxine Watson is Associate Professor of Biology at Indiana University.

Her dissertation was designed to test whether plants exhibit niche partitioning in ways similar to those of animals. She showed that closely related moss species differ between genera, and she did the first age-structure analysis for lower plant populations (182). Her innovative research on higher plants examined the interplay between physiology, development, and demography (183). In this work she showed that plants differ from animals due to constraints imposed by their vascular structure; since costs are thus expressed in regard to an integrated physiological unit and may be self-supporting, the limiting resource in plants may often be meristems rather than nutrient or carbon resources. Although unmarried, Watson has an adopted daughter. During a period of serious ill health, she continued to direct many graduate students, and she is now moving actively toward innovative studies of the interplay between developmental phenology and environmental variation in determining plant demographic responses (184). Her goal is to provide foundation papers for the emerging subfield of developmental ecology.

A leader who added novel approaches to the 1970s advances in plant population ecology, Patricia Werner took her PhD in 1972 at Michigan State University, where she remained and rose to Professor of Botany and Zoology. Through analysis of plant characteristics (sessile, "plastic" growth) in field experiments, she modeled population dynamics and calculated population growth rates using mathematical tools developed for animal populations. Her paper demonstrating that the size of the plant is more important than its age in determining its demographic fate led to changed thinking about plant life histories and became a citation classic (185). In research on plant populations in successional environments, she not only captured the ideas of the mid-1970s by incorporating the exciting conceptual advances from recent field experiments, but she put these in the context of the interaction of life history characteristics with a changing environment—thus laying out the applicability of competition theory of the time for plant populations (186). Research on colonization of biennial species formed the basis of her thinking about plant communities and underlies many of the subsequent conceptual and empirical studies developed by her graduate students (who include four women) at Michigan State (187). Werner was elected an ESA Council member (1979) and President of the International Society for Plant Population Biology (1988). Offered the challenge of building a modern research center in the Australasian tropics, in 1985 she became Director of the Tropical Ecosystems Research Center for CSIRO in Darwin, Australia, following which she became Director, Division of Environmental Biology of the National Science Foundation (1990 to 1992). She currently is Professor and Chair of the Department of Wildlife Ecology and Conservation as well as Director of the Center for Biological Conservation at the University of Florida, Gainesville.

An untimely death in 1987 cut short one of the stars among plant population ecologists. Deborah Rabinowitz, a 1975 PhD from the University of Chicago, became the first woman Assistant Professor in the Ecology and Evolutionary Biology Department at the University of Michigan, and subsequently Professor in the Section of Ecology and Systematics at Cornell University. A key characteristic of her research was its "unusual slant on an old problem" (161, p. 86). Her major research fell into three groups: 1) mangrove distribution, in which she analyzed the early growth of mangrove seedlings in Panama with an hypothesis concerning the relationship of dispersal and zonation (141); 2) studies of rarity including empirical studies of rare prairie grasses, aimed at explaining these plants' peculiar ecology (143); and 3) concepts of rarity, in which she clarified its meaning with a classification of rare species based upon range of geographical distribution, degree of habitat specificity, and local population size (142). Rabinowitz was widely recognized as a role model by many younger women ecologists (81). Her obituary said, "she possessed a combination of qualities that are nowhere common. She was among the rarest of the rare" (161, p. 87).

Women Ecologists Studying Animal Behavior

Although the 1987–1988 ESA Survey (185) showed relatively few women studying animal behavior, this may reflect that some women in this field are not members of ESA. Among the ESA membership, Martha Crump, Susan Riechert, and Judy Stamps represent different areas of animal behavior.

Martha Crump, Adjunct Professor of Biology at Northern Arizona University (1974 PhD, University of Kansas) is one of the few women behavioral ecologists whose work has centered on reproductive ecology with tropical amphibians. The first long-term ecological research on a community of tropical amphibians was hers on an Ecuadorian community with the most diverse variety known of reproductive modes in amphibians (41). Her research has been recognized widely as the first to take a community ecology approach to reproductive strategies. Furthermore, she presented a new way of thinking and looking at variability in amphibian egg size (42), a variability that she examined in five species of tree frogs (*Hyla*) as a function of habitat predictability. Crump is married to another tropical field ecologist, and they have two children. Whenever possible, the children accompany and assist their parents in the field (to date in Costa Rica, Ecuador, Colombia, and Argentina). As a Professor at the University of Florida, Gainesville, Crump assured her female graduate students that "field biology and family can be a wonderful, successful union" (M Crump, personal communication). Crump and her ecologist husband decided to leave full professorships at the University of Florida after 16 years to become more involved in field conservation projects and teaching ecology and conservation in Latin America. During the school year they alternate their trips so that one parent stays home with the children. Crump says, "I still see my contribution as a role model for women (in this country and Latin America) who want to combine family and field work. The key is having a supportive husband" (M Crump, personal communication).

A spider population biologist, Susan Riechert, Distinguished Professor of Zoology, University of Tennessee-Knoxville, has a 1973 doctorate from the University of Wisconsin-Madison. She was introduced to natural history at an early age by activities centered on insect collections and trips to local ponds and woods with her grade-school friends. Her career working with spiders was launched from a field zoology course that ultimately led to research on the population biology of a funnel-web-building spider (148), which she has extended to include the evolution of cooperative spider behavior. Since spiders are among the few organisms that lend themselves to testing evolutionary game theory, her series of papers and a review of this theory have gained much attention (151). She also tested the hypothesis of potential limiting effects of gene flow on adaptation with experiments in desert spiders (149), in which she investigated a reason for population deviation from adaptive equilibrium. Riechert has been interested in spider assemblages in managed habitats and recently worked on limiting effects of generalist predators as agents of biological control (150). She discovered manipulations that conserve spider communities in agroecosystems and decrease by 60–80% the plant damage caused by grazing insects. Riechert was elected President of the American Arachnological Society (1983) and a Fellow (1993) and President-Elect of the Animal Behavior Society (1994).

Judy A Stamps, Professor in the Section of Evolution and Ecology, University of California, Davis, received her PhD (1974) at the University of California, Berkeley, where she obtained a strong background in ethology that enabled her to think about problems simultaneously at the proximate and ultimate levels. She rediscovered an idea mentioned by early workers (including Margaret Nice) that newcomers in territorial species prefer to settle next to established territory owners (168). This work alerted ecologists to a behavioral process with important implications for reintroduction programs in conservation biology. She wrote the first paper on parental behavior in birds that suggested avian behavior might be as complicated as that of primates and other mammals (167). Stamps also presented a review (169) using her lengthy series of studies on habitat selection and territoriality in juvenile lizards to illustrate a series of assumptions about territorial animals that are widespread in the literature, but as yet poorly tested. Stamps has been recognized in the Animal Behavior Society as a Fellow (1991) and with their Exemplar Award (1994).

Women Marine Ecologists

Although marine ecology has a long history, American women were slower to enter this area than terrestrial ecology. Deborah Dexter, Professor of Biology, San Diego State University, earned her PhD (1967) at the University of North Carolina. Her area of specialization is marine benthic ecology, especially community structure and population dynamics of dominant species on intertidal sandy beaches. Her research has spanned six continents, and she recently has synthesized 30 years of her own work, along with the last 25 years of literature, about sandy beaches throughout the world (48). She explains why the generalization that diversity increases with tropical habitats is apparently not true for sandy beaches. In a way similar to Catherine Keever, Dexter has continued to carry out research despite her choice to remain at an institution where her major commitment is to teaching.

Sarah Ann Woodin has a 1973 doctorate from the University of Washington. She was an Assistant Professor at the University of Maryland and Johns Hopkins University (1972–1980) prior to marrying and going to the University of South Carolina. She was a Research Professor in the Marine Science Program there before being promoted to Professor of Biology and Marine Science (1987). Much of her research on marine benthic communities has centered around adult-larval interactions. In an early paper she summarized data supporting the importance of interactions between adults and settling larvae or newly settled juveniles in determining the composition of the assembly of infaunal communities (196). Her predictions regarding assemblage characteristics and recruitment success or failure, given the importance of adult-larval interactions, have led to much subsequent research by others. Woodin significantly highlighted the importance of biogenic structures to the composition of the assemblage (197), and she also focused attention, through a series of experiments, on disturbance by organisms and physical forces. More recently she designed an elegant laboratory and field demonstration of the effect of haloaromatic compounds on recruitment (198).

Jane Lubchenco, Wayne and Gladys Valley Professor of Marine Biology, Oregon State University, has a 1975 PhD from Harvard University; she became the first woman Assistant Professor in the Harvard Department of Biology (1975–1977). Lubchenco and her husband went to the Zoology Department at Oregon State University in 1977 with a split position, which worked particularly well while their children were very young (98). They later were elevated to full-time appointments, and now each has been named to an endowed chair in marine biology. She has written that "our philosophy [her husband's and hers] has been that one needn't sacrifice family for career or career for family. Academic couples need to have more CHOICES, more OPTIONS for combining careers and families. For us, combining both in a sane manner meant doing each part-time. Because we were both committed to doing this, it has worked well—beyond our expectation" (J Lubchenco, personal communication).

Lubchenco's research has been directed toward linking ecological patterns and processes occurring at different scales and different levels of organization in rocky intertidal communities. In a paper (95) from her dissertation, which became a citation classic, she experimentally showed that the effect of herbivores on intertidal diversity depended upon the interaction between the food preferences of the herbivores and the competitive abilities of the macroalgae. Jane and her husband often conduct separate but parallel and complementary research projects, with each approach enriching the understanding of the other. One of their collaborative studies (108) draws on comparable experiments conducted in two temperate rocky intertidal communities (Pacific Northwest and New England) and a tropical one (Pacific coast of Panama). The latter is different in lacking a keystone species—characterized instead by a diverse suite of consumers at all trophic levels, each of which can compensate for the removal of the others. Lubchenco presented a new synthesis of plant-herbivore interactions by reviewing marine plant–herbivore ecology (97) and developing a theoretical model for linking ecological patterns and processes from the individual to the population, community, and biogeographic scales. She was the first to propose a mechanism to explain the alternation of morphologies of different phases of seaweeds with complex life histories (96). As is true of many ecologists today, she increasingly is directing her efforts toward resolving the pressing environmental challenges facing humanity. Although the first author on another citation classic (99), known as the Sustainable Biosphere Initiative (SBI), she indicates that the paper resulted from the "collaborative wisdom" of ecologists who served on the ESA Research Agenda Committee. SBI calls ecologists to action in creating the knowledge needed to address urgent ecological problems. Lubchenco serves on numerous national and international boards and panels. Among her many honors are election as the fourth woman President of ESA (1993), as a Fellow in the American Academy of Arts and Sciences (1993), as a John D. and Catherine T. MacArthur Fellow (1993), and as President of the American Association for the Advancement of Science (AAAS) (1996).

CONCLUSIONS REGARDING SUCCESSFUL WOMEN ECOLOGIST DOCTORATES (1900–1975) IN GENERAL COMPARISON WITH POST-1975 DOCTORATES

Personal Characteristics in Common

All of the women discussed were highly motivated. A survey of the living pre-1976 graduates (81) indicated they were motivated almost universally by a childhood interest in nature and doing outdoor activities while growing up, sometimes through scouting. Some also mentioned the influence of teachers, particularly at women's colleges. Of the post-1976 graduates in this survey, 44% indicated the importance of childhood influences, but an equal number pointed to undergraduate courses, 16% to field station experience. The increased motivation derived from ecology courses parallels their increased availability during the 1960s and 1970s (81).

Other prime characteristics clearly necessary for success are willingness to work hard and to persist in doing so. Some sociological studies suggest that positive women role models have a significant impact not only on motivation and career decisions but on the persistence for ultimate success (104). Although most of the pre-1976 PhD women ecologists succeeded without women role models, other support mechanisms were crucial for their persistence to overcome obstacles. For some single women collaboration with relatives or friends provided support (e.g. Braun, Keever, and Quarterman), and in the earlier period this also made some kinds of field work feasible (81). Marriage in some cases has provided this support, i.e. a husband to work with as a team (Baskin and Lubchenco) or to encourage persistence in research (e.g. Shreve, Nice, Crump, Zedler, and Ewel). Assistance with family responsibilities is also important, as managing simultaneously career, marriage, and motherhood demands persistence that is based on adaptability and high levels of energy, enthusiasm, and endurance. However, as discussed in other sections, marriage can lead to problems.

Women frequently have been assisted in their professional struggles by concerned male ecologists who served as mentors. Otherwise, many women would have been unable to progress as far as they have (despite the recent development of a larger group of women ecologists). The lack of role models is still considered by some (104) as an important impediment in the professional advancement of women scientists. However, Brattstrom (18, p, 143) recently suggested "There are role models out there, we just need to talk more about them! . . . And we need to start it now!" Among ecologists, Brattstrom mentions only Nice, but in the context of his remarks, this paper presents a number of possible role models who have been ignored or perhaps undervalued.

Graduate Education

By the turn of the century, women were obtaining PhD degrees in ecology in the major American universities where it was developing as a research field. Along with the expansion of ecology during the 1960s and early 1970s, a corresponding increase occurred in the numbers of women ecology PhDs and of institutions where they were granted. From 1976 to 1987 there was a pronounced increase in women PhDs in ecology throughout American universities, e.g. at Cornell they increased from 11% to 25% (B Peckarsky, personal communication). Increases also occurred in Ecology Programs that generally were established in the 1970s, the period with the greatest number of ecology doctorates (men and women). In fact, the 1980s are a significant period for women doctorates at some universities. For example, women constituted 44% in the University of Minnesota Program (M Davis, personal communication). At Duke University, in Botany, there was a dramatic increase from 12% on average for the previous 38 years to 60% in the 1980s (Billings and Antonovics, personal communication). Indeed, the greatly increased numbers of women doctorates produced in major ecology programs during the late 1970s and into the 1980s precluded my presenting the contributions of women ecologists who obtained their PhD degrees after 1975.

Subfield of Ecology Entered

Women with pre-1960 degrees tended to study plants, either physiologically or in populations and communities (Table 1). Furthermore in a general survey in 1987 of all ESA members, with 3100 responding, 49% of women still indicated plants were their "organism of choice" for study (181), whereas only 37% of males did so. Similarly, 54% of a 1987 survey of 200 established women ecologists with post-1975 degrees were working with plants (81). Studies of animal behavior, marine ecology, and mathematical and systems ecology increased somewhat for successful women with degrees in the 1960s and 1970s (Table 1). In the 1987 ESA survey, some subfields had a similar percentage of males and females (e.g. community ecology, empirical ecosystem studies, and plant physiological ecology), whereas others exhibited dichotomies between the genders. For example, 11% of the females indicated plant population ecology as their best descriptor, whereas only 3% of the males did so. Four percent of the males indicated animal behavior, whereas only a negligible fraction of females did (181).

Permanent Employment After Degree

Many women ecologists with pre-1976 PhD degrees found it difficult to obtain jobs commensurate with their education, especially if they were married. In fact, this has generally been a difficulty for women in science in the past (1). Despite progress, some of these problems continue, as l7% of the total women and 58% of those who were women respondents in the 1992 ESA survey indicated they were not employed as ecologists due to family constraints (85). On the other hand, 29% of the total number of women indicated unavailability of positions in their area of expertise, and another 28% a change in professional interests, as the reasons for being unemployed. However, women progressively have gained positions in major research-oriented universities, and the increasing number of these women with degrees from 1961 to 1975 (the "first modern wave") who married and had children indicates increased possibilities of working out arrangements to combine family and career (Table 1). For example, more attention is being given to the complex problem of two-career marriages (common among ecologists), with various approaches to a solution (98). In a 1990 survey of women ecologists (62), with respondents primarily from large, research-oriented universities, women in dual-career couples (where the woman often takes a soft-money research position), and to a lesser extent those who share positions, have reduced access to resources that facilitate research creativity and productivity. These women further indicate psychological stress from being considered "second-class citizens" because they are "the trailing spouse" (62, p. 150). Some encouraging news comes from women at institutions where policies have become favorable for women to attain full professorships (e.g. Zedler, Ewel, Porter, Woodin and Lubchenco); discouragingly, stubborn problems still persist for other women (e.g. Baskin with an Adjunct Professorship and Fox with a long-shared professorship).

Women, married or single, generally have faced salary inequities that continue today. Salary disparities still occur in some age classes and categories as shown in the ESA 1987–1988 membership survey (181). In the ESA 1992 survey, salary comparisons by age and gender indicated that male respondents earn nearly $6000 more per year than female respondents of the same age (84). Comparisons of income by time since highest degree and gender show that males make $4600 more than females who completed their education the same year. These lower salaries occur at all levels of professional experience (84, 86).

Publication Record: Numbers, Citations, and Recognition as Classics

Recent studies of established scientists have documented that women are less "productive" than men as defined by number of papers published and number of citations. Several studies have focused specifically on ecologists because of the large number of graduate students and comparatively large representation of women (92). One study did not detect significant differences in productivity between men and women (166) , but these results were questioned because of the small sample size and lack of comparisons of academic age and rank (93).

Subsequently, Primack and O'Leary (136) analyzed a large sample of pairs of men and women ecology graduate students who participated in an Organization of Tropical Studies (OTS) course between 1966 and 1979. They used Science Citation Index (1980–1984) to determine the total number of ever-cited publications written by each individual during his/her scientific career. One of their most striking conclusions is that women are unrepresented in the top group of researchers. Whereas women had an average of 47% as many publications that were cited an average of 43% as much as publications by men, the gender difference disappeared when the most productive 9% of men were removed from the analysis. Then no average difference existed in number of cited papers of 91% of the men compared to all of the women. Thus, Primack and O'Leary questioned whether "differences in productivity might be better framed to ask why a small proportion of male scientists are extremely productive" (136, p. 11).

In an extension of the previous OTS studies to include participants from 1966 to 1986, Primack and Stacy (138) confirmed that productivity of women ecologists generally was lower than their male counterparts. However, significantly, most of this difference apparently resulted from a lower percentage of women who continue careers that involve research. Analysis of the group of women who continued by publishing at least one paper indicated that these women are approaching rates of publication and accumulated citations equal to those of the men. Another interesting contrast is that the productivity level of women among the OTS participants trained between 1966 and 1975 (within the same time frame as the "first modern wave" of selected, highly successful women in my discussion) is only about 60% of that of men. On the other hand, women trained from 1976 to 1986 were attaining about 80% to 90% of the productivity level of men. Furthermore, several older women ecologists, in contrast to the men, in the OTS group are "late bloomers" in that they became highly productive after an initial delay. Another indication of increasing productivity of younger women is their ability to achieve their first publication earlier than men.

Although women wrote many significant papers from 1947 to 1979, only two women's names appear among 105 authors or coauthors of the 80 Ecological Citation Classics 53 (ECC) selected by McIntosh (107) during this 30-year period. McIntosh, however, admits his bias in selection of papers published by Current Contents as being ecological, i.e. based on subject matter, recognizable ecologists, and journals known to publish ecological articles. He further suggests that the initial basis of citation frequency does not necessarily express intrinsic merit of a publication and is only one measure of a classic article. Everyone is aware of important advances being published and ignored, only to be recognized much later as classic contributions to science. McIntosh (107, pp. 37–38) quizzically notes, "Most striking is the absence among these [ECC] authors of some very famous names, names that by all criteria belong in the pantheon of ecologists (e.g. GE Hutchinson, RH McArthur, RM May, EP Odum, TW Schoener, RH Whittaker, among others)." He did not know "whether their many articles were actually not cited frequently or whether they chose not to provide the requested biographical statements" that allowed them to be credited as authoring a citation classic. If the giants of ecology listed above have not produced an ECC, perhaps there should be less concern that so few women appear in this study.

On the other hand, it is obvious from this historical review that women with pre-1976 PhD degrees have been publishing papers with the same characteristics as those indicated by ECC authors as a basis for the frequency of citations of their selected articles (107). For example, women have been pioneering ideas and methodologies in subjects of rising interest (e.g. Patrick, Bentley), presenting mathematical approaches (e.g. Pielou), and challenging current dogma in several subfields (e.g. Nice, Willson, Langenheim, Rathcke). In some cases their work became a citation classic (e.g. Fox, Werner, Lubchenco, Myers), and one by Davis was included in a 1990 collection of "classic papers" (147), whereas other women's research has not been recognized for the impact it actually may have.

Recognition

Although opportunities did not come easily to the majority of early women ecologists, they did become members of the Ecological Society of America. Six percent of charter members of ESA in 1915 were women; by 1931, 9% were women, of whom 36% had PhDs (81). Women ecologists claimed full membership, attended banquets, and did not have to present their papers in separate sections—they were not excluded as they were in some other professional societies (e.g. American Chemical Society, Geological Society of America) (154). However, progress was slow from 1915 to 1987 in recognition of women through awards and election as officers, commensurate with their accomplishments and their number in ESA (81). Among the "early pioneers," only Braun was recognized. Among the "late pioneers" are Patrick, Langenheim, and Davis, but there is a perceptible increase among the "first modern wave" with Pielou, Sharitz, Werner, Bentley, Morrow, and Lubchenco. Because of the breadth of ecology, some women ecologists have been recognized by being elected as presidents of related societies (e.g. Moore, Nice, Patrick, Leopold, Davis, Langenheim, Werner, James, Christensen, and Stewart). Prestigious awards, other than those from ESA, have been given to Nice, Carson, Patrick, Davis, Leopold, Willard, and Lubchenco.

To the extent that women receive it, major recognition (e.g. presidencies of societies and the most prestigious awards) would be expected to go to the longer established women in the pre-1976 doctorate category. However, there are encouraging signs for the future in the recognition of women with ESA awards specifically given to younger ecologists. Women have received 61% of ESA's Murray F. Buell Awards for the best paper presented orally and 88% of E. Lucy Braun Awards for the outstanding poster—each given at the Annual

Meeting by an undergraduate or graduate student or a person with a doctorate who has completed defense of thesis within the previous nine months. From 1948 to 1978 there was no woman recipient of the George Mercer Award, given annually to an ecologist under 40 years of age for an outstanding paper published within the past two years. However, from 1979 to 1995, women received almost a third of the awards.

The number of women invited to be members of the editorial board of ESA journals and to participate in symposia at ESA annual meetings has been considered recently. Duffy and Hahn (50) pointed out the relatively low numbers of women on the ESA editorial boards (1980–1993) and questioned whether male dominated boards could contribute to women's lower productivity. Gurevitch (61) demonstrated that women were less likely to be symposium speakers at the 1987 ESA meeting when only men solicited speakers. However, Crowe and King (40) found an increase in the last 10 years in the proportion of women who were first authors in both contributed sessions and symposia in annual ESA meetings. By 1993, the earlier bias (61) of some male organizers in not inviting women speakers apparently had vanished. Crowe and King optimistically suggest that these "results indicate that gender representation can change relatively rapidly and easily" (40, p. 373).

General Comments Regarding Progress

Considerable strides have been made by women ecologists since the turn of the century. Although most overt institutional discrimination policies that older women faced are no longer in place, various "microinequities" may affect the recruitment and particularly the performance of younger women scientists (65). Since 42% of the 21–25 year age group of the 1992 ESA membership is female, recruitment of women into ecology does not appear to be a current problem (84). The progress made in this age group is strong, considering that women over the entire age range of membership make up only 23% of the Society (84). This survey, nonetheless, suggests that it may still be more difficult for women than for men to secure employment in the field, and some of this may relate to problems associated with marriage or family (85). Thus for future increases in the proportion of employed women ecologists, better ways will be needed to combine family and job responsibilities and to find solutions to the difficult career decisions that face dual career couples.

In academia (where most ecologists are employed), male ecologists on average publish more papers, have higher salaries, achieve higher academic positions, and feel generally more successful in their professional lives than do female ecologists (137). Primack and O'Leary concluded that these differences cannot be explained solely by whether the women were married and had children, or by gender differences in attitudes toward careers or time devoted to research; further, women at all stages of their careers face a constant, low-level disadvantage that prevents their competing as successfully in academia as men do. Women ecologists may often face a series of disadvantages early in their careers, leading to lack of recognition that decreases motivation and may eventually stifle high professional attainment and productivity. If a woman succeeds in obtaining a good academic job, she often lacks senior mentoring relationships, which can be crucial in a complex institutional environment. In sum, Primack and O'Leary (137) indicate that these individual disadvantages may seem minor at first because they are temporary and not obviously related to productivity. In fact, the advancement of women ecologists may still be limited due to accumulation of disadvantages and accompanying missed opportunities. Three years later, however, Primack and Stacy (138) add an optimistic note—that various changes in the social climate regarding women ecologists have been crucial in an increasingly positive trend for women to become some of the most productive and honored individuals among the younger generation of ecologists.

Although problems persist for women ecologists, the issues of gender equality in professional development are now being put forward, meaning that they can be more clearly recognized and addressed. This was not the case for the "early women pioneers" nor for the "late women pioneers" until quite recently, or even for the "first modern wave." Thus, these ecologists deserve all the more credit for opening the path with their research contributions, despite many obstacles.

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