

Biographical History of Behavioral Neuroendocrinology

CHAPTER 29

C SUE CARTER

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Key words: monogamy, social bonding, vasopressin, oxytocin, prairie voles, Kinsey Institute

Summary. C. Sue Carter was born in 1944 and grew up in rural Missouri. She earned a BA in Biology from Drury College, which was located a few miles from her family home, and then a PhD in Zoology from the University of Arkansas. It was during her post-doctoral fellowship at Michigan State University that she first became engaged in behavioral neuroendocrinology research. Over the subsequent five decades Carter held professorships at six universities and served as Director of the Kinsey Institute; each change in institution expanded her scientific interests and added depth and complexity to her research program. She is perhaps best known within behavioral endocrinology for (1) introducing prairie voles as a model organism for studying the physiological regulation of social bonds and biparental behavior and (2) for catalyzing the study of oxytocin and vasopressin in behavior. However, she also has published extensively on the importance of oxytocin in promoting human social behavior, and the behavioral consequences of aberrant oxytocin signaling. Lastly, Carter was an exceptional mentor to trainees and colleagues, and the strongest possible advocate for women and individuals from groups underrepresented in science and academia.

29.1 Early Life, Education, and Training

Carol Sue Carter, professionally known as C. Sue Carter, was born on 25 December 1944 in San Francisco, California. Her father was working in the Kaiser Shipyards at that time. She claims that without consulting her, the family migrated back to their original home in the Missouri Ozarks when she was 3. There she grew up immersed in rural America, in turn developing the work ethic and fierce determination that would propel her through the inevitable ups and downs of academia. Carter was a middle child of eight offspring spread over a 27-year period, so she claims the advantage of being the recipient of a great deal of alloparenting. Throughout middle school and high school, she raised cattle to save money for her college education.

Carter attended Willard High School in Willard Missouri and then earned her Bachelor of Arts degree at Drury College (now Drury University) which was located approximately 10 miles away in Springfield, Missouri. She graduated *summa cum laude*, with a major in Biology. In recognition of her extraordinary career, Drury University awarded Carter the 2016 Distinguished Alumni Award for Life-time Achievement.

After leaving Drury, Carter pursued a PhD in Zoology at the University of Arkansas. Upon matriculation, her goal was to complete a two-year master of science degree and then teach high school. However, the course of her future serendipitously changed when she was awarded a three-year NSF predoctoral scholarship, with the understanding that she would complete a PhD in that time period. She accomplished this under the joint mentorship of Douglas A. James, a conservationist with expertise in avian ecology and ethology and Jack Marr, a behavioral biologist, whose interests lead her to do a thesis entitled “Early olfactory experience in the guinea pig, *Cavia porcellus L.*” This graduate work formed the basis of Carter’s first two publications in *Animal Behavior* (Carter & Marr, 1970; Carter, 1971) on developmental aspects of olfactory imprinting preference; the work cemented her love of research and desire for an academic career. A shift toward studying hormonal mechanisms of behavior began as she launched her post-doctoral training at Michigan State in the laboratory of Lynwood G. Clemens (Chapter X). Clemens had trained with Frank A. Beach (Chapter X), Robert W. Goy (Chapter X) and Roger A. Gorski (Chapter X), and this training brought her into the field of behavioral endocrinology. At the time that Carter joined his lab in 1969, Clemens was studying the effects of early life exposure to gonadal steroids on adult reproductive behaviors in rats. Carter brought hamsters to that laboratory as well as a comparative and developmental perspective on sexual behavior that she retained throughout her career (Carter et al., 1972). In 1970, Carter married Stephen W. Porges (a psychologist) and moved with him to West Virginia University (WVU). At WVU, she was sponsored by Martin Schein for an independent NIH Postdoctoral Fellowship. There she also expanded her research to include hormonal regulation of post-copulatory sexual receptivity (Carter & Schein, 1971), quickly establishing herself as an expert in hormones and sex behavior, and initiating her transition to research independence.

29.2 Institutions, Promotions, and Leadership Positions.

Carter and Porges relocated to the University of Illinois, Urbana-Champaign in 1972, where she was offered a research position in a newly formed laboratory for psychopharmacology sponsored by the State of Illinois Department of Mental Health. During this period, Carter developed and taught a popular elective seminar in Human Sexuality; it was the first time this subject had been offered at that university and it attracted more than 200 undergraduate students.

In 1974, largely through the efforts of Ed Banks, a senior ethologist, the University of Illinois created a faculty position for Carter which consisted of appointments in three separate units. She began her faculty career as an Assistant Professor in the Departments of Psychology, Ecology Ethology, and Evolution, and the School of Basic Medical Sciences. She rapidly rose through the ranks to attain Professor in 1984. It was during this period that three crucial shifts in Carter's research occurred that would shape the next several decades of her career: (1) she began to direct her work to the emerging field of behavioral neuroscience and to studies of sex differences in the brain (Greenough et al 1977), (2) she incorporated increasingly broad measures of social behavior in a multitude of species, including lemmings (Huck et al., 1979), and (3) she began to collaborate with Lowell Getz, a mammalogist working with prairie voles (*Microtus ochrogaster*; Dluzen et al., 1981).

At that point in time, prairie voles had rarely been studied in the laboratory and their mating system (social monogamy) was unknown. Carter's first several prairie vole studies examined basic reproductive biology and confirmed that females responded to ovarian hormones in a way that was similar to other induced ovulators (Dluzen and Carter, 1979). However, this species did not exhibit an estrous cycle and was uniquely dependent on social cues for reproductive activation, which was initiated by male pheromones (Carter et al., 1980). Social cues in turn precipitated a cascade of endocrine events in the olfactory bulb that implicated the vomeronasal organ in the facilitation of reproduction in this species (Dluzen et al., 1981). However, it was Carter's interactions with Professor Lowell Getz, a behavioral ecologist who conducted population studies on several species of *Microtus*, that prompted her to begin thinking about reproductive behavior in the context of a monogamous social system. The early papers by Carter and Getz describing the social organization (Getz & Carter, 1980) and mating system (Getz et al., 1981) of prairie voles laid the groundwork for Carter's research developing prairie voles as a model for studying the physiological mechanisms underlying the formation of adult social bonds and parental care. Carter and Getz published several additional experimental papers and highly cited review papers on monogamy and pair-bonding over the subsequent twenty years (for example, Carter et al., 1995). Getz remained an engaging colleague, good friend, and reliable source for outbreeding Carter's prairie vole colony for decades.

Toward the end of her time at Illinois, and despite being the mother of a one-year old baby, Carter took a research sabbatical in the Physiology Department at Stanford University (1981). She worked primarily with Julian Davidson, a renowned behavioral endocrinologist who was one of the founding editors of the journal *Hormones and Behavior*. Davidson was remarkably effective in translating fundamental rodent research into the study of hormones and sexual behavior in men and women. Carter's first forays into clinical research were studies with Davidson on the effects of age and menstrual cycle on the sexual arousability of women (Morrell et al., 1984) and the effects of testosterone replacement on tactile sensitivity in hypogonadal men (Segraves et al., 1985). The latter human studies extended into a collaboration with Davidson that continued into the early 1990's (Burriss et al., 1991), a time during which Davidson took a one-year sabbatical to NIH.

Shortly after returning from Stanford, and while still on the faculty at the University of Illinois, Carter served a one-year rotation (1982-1983) as a Program Officer in Psychobiology at the National Science Foundation, in Washington DC. She used her position to advocate for increased funding for research on the biological bases of behavior and greater support of interdisciplinary research. She also used that period to gestate a second child, returning to Illinois

in time for his birth. However, Carter's work inside the beltway had precipitated a case of what she refers to as "Potomac Fever", a common, but noninfectious disorder characterized by the realization of the importance of federal funding for the growth of science. It was an increased awareness of opportunities to collaborate with government laboratories and a personal desire to raise their family in a less extreme climate than that offered by central Illinois that prompted Carter and Porges to begin considering faculty positions in the Washington area.

Thus, soon after being promoted to Professor at Illinois (1984), Carter left to join the Department of Zoology at the University of Maryland, College Park (1985). Diane Witt, who had worked with Carter as an undergraduate honors student in Illinois, moved with her to Maryland to pursue a PhD. Witt's thesis research centered around behavioral and hormonal factors influencing estrus induction in prairie voles. In 1990, Witt and Carter published their first paper examining the effects of oxytocin on social interactions and sexual behavior in prairie voles (Witt et al., 1990). It was the first of more than 125 papers Carter has published on oxytocin to date and was a harbinger of her extensive exploration of the neuroendocrine mechanisms underlying pair-bonding (described in more detail in section 29.3). Carter was appointed Distinguished University Professor at the University of Maryland in 1997 in recognition of her scholastic achievements, including her role in mentoring trainees and other scientists, often beyond her own field. She was the first woman at the institution to be awarded this distinction.

During her tenure at the University of Maryland, Carter also was a Guest Researcher within the Developmental Endocrinology Branch of the National Institute of Child Health and Human Development at NIH. Through collaborations with George Chrousos, Philip Gold, and Margaret Altemus, intramural NIH clinician-researchers with expertise in neuroendocrine and behavioral sequelae of stress, Carter began studying the effects of stress and immune function on women's mental health. She also collaborated with Chrousos on studies of reproductive success in common marmosets (*Callithrix jacchus*), a highly social primate species, and the effects of lactation on stress reactivity and immune function in post-partum women. These interactions also added a new layer to Carter's prairie vole research as she explored the hypothesis that improved stress regulation was a consequential benefit of social bonding and mediated by oxytocin. It also brought to her attention the physiological "peculiarities" shared by prairie voles (Taymans et al., 1997) and socially monogamous species of New World monkeys (Johnson et al., 1986), in turn prompting her to speculate that there were likely common physiological mechanisms underlying social monogamy across mammalian species (Carter & Perkeybile, 2018).

After 16 years at Maryland, Carter and Porges were recruited back to the University of Illinois, this time to the Chicago campus, to serve as Co-Directors of the Brain-Body Center and Professors of Psychiatry. Carter's research during that period was well-funded by a series of NIH Program Project grants and R01s. In addition, in collaboration with Dr. Porges, she helped create a large NIH renovation grant that they used to fund a 20,000 sq foot laboratory, facilitating the integration of basic and clinical research. Carter also developed novel assays for the noninvasive measurement of oxytocin in human saliva, which are now widely accepted and used. During this period Carter continued to collaborate with and to mentor clinicians focused on various aspects of psychiatry and child development, including Suma Jacob, MD, PhD. Jacob was a child psychiatrist, originally trained by Martha McClintock, who had an interest in studying oxytocin in the context of autism. Together, Jacob and Carter did the first study of genetic variation in the oxytocin receptor in Caucasians with autism, published in 2007 (Jacob et

al., 2007) and widely replicated. Jacob is now a chaired professor at the University of Minnesota and the role of oxytocin in autism continues to be a major topic of research in psychiatry.

While oxytocin effects on behavior remained central to her research, the emphasis of Carter's research at UI Chicago shifted to understanding the importance of developmental exposure to oxytocin and vasopressin on physiological responses, brain development, attachment, and bonding. She conceptualized oxytocin signaling, and its modulation of stress responses, as an important mechanism through which disruption of parent-offspring and adult-adult bonds could promote pathology. Carter published several papers supporting a link between oxytocin and vasopressin and symptom severity in patients with schizophrenia (e.g. Rubin et al., 2010) and proposed that dysregulation of oxytocin also could underlie the skewed social behaviors that are characteristic of autism spectrum disorders (e.g. Jacob et al., 2007) and Williams Syndrome (e.g. Dai et al., 2012). She also became involved with projects on the role of oxytocin and birth-experiences in postpartum depression through collaborations with a clinical research group at McGill University in Montreal (e.g. Zelkowitz et al., 2014).

From 2013-2014, Carter spent a brief period as a Professor of Psychiatry at the University of North Carolina, Chapel Hill, before being recruited to Indiana University as the Executive Director of the Kinsey Institute and the Rudy Professor of Biology. The world-renowned Kinsey Institute was established at Indiana University in 1947 to promote understanding of human sexuality, gender, and reproduction through historical preservation of documents and art, research, education, and outreach. As director of the Kinsey Institute from 2014 to 2019, Carter made the bold move to expand, for the first time, the Institute's emphasis beyond sex, gender, and reproduction to include the context of relationships, specifically the psychological and emotional functions and contributions to well-being. Carter argued that sex can have very different meaning and elicit very different psychological and physiological responses when it occurs consensually within a relationship, consensually outside of a relationship, or without consent. She also proposed to increase research at the interface of medicine and sexuality, and to build further on the study of how physical and psychological trauma can alter sexuality.

She was the first biologist to be appointed director since Alfred Kinsey, who likewise trained as a zoologist. Some critics interpreted this pivot toward sex in the context of relationships by a director who studied monogamous rodents as an attempt to sanitize the Kinsey Institute and bow to political pressure; nothing could have been further from the truth. Those leveling this criticism do not appear to have read or truly understood Carter's work, which emphasized that prairie voles were socially, but NOT sexually, monogamous. Furthermore, Carter had built her career on studying the overlapping and diverging physiological mechanisms involved in sexual behavior, social bonding, and parental behavior in prairie voles, and had applied her knowledge to understand disorders characterized or exacerbated by disrupted social behaviors. Alas, for an institute that is very comfortable when mired in controversy, expanding its mission to understand love may have been a step too far for the Kinsey Institute. In 2019, Carter completed her term as Director of the Kinsey Institute and returned to full time research, as a Distinguished University Professor. The current director of the Kinsey Institute replaced "love" with "sexuality" on the Kinsey Institute website but retained the emphasis on relationships and well-being.

In 2021 Carter was offered a position as a Professor of Psychology at the University of Virginia. At UVA Carter has merged her research program with that of her epigeneticist collaborator, Jessica Connelly (Bell et al., 2015). Carter and Connelly have worked together for more than a decade, with current R01 funding from NICHD. Their program continues to study both prairie vole and human behavior. It also focuses on the developmental effects of early social experience, a consistent theme throughout Carter’s career. In addition, Carter and Connelly are refining noninvasive methods for measuring peptides and peptide receptors, which can be used in behavioral research, including many translational studies, and are becoming accepted as “biomarkers” for wellness and longevity. Thus, this most recent phase of her academic journey studying longevity began when Carter was in her mid 70’s, yet somehow seems fitting for someone whose first published research paper appeared in 1970.

Table 1.

Years	Position	Department	University
1974-1977	Assistant Professor	Ecology Ethology, and Evolution & Psychology	University of Illinois, Champaign
1977-1984	Associate Professor	Ecology Ethology, and Evolution & Psychology	University of Illinois, Champaign
1984-1985	Professor	Ecology Ethology, and Evolution & Psychology	University of Illinois, Champaign
1985-1997	Professor	Zoology	University of Maryland, College Park
1997- 2001	Distinguished University Professor	Biology	University of Maryland, College Park
2001-2012	Professor	Psychiatry	University of Illinois, Chicago
2013-2014	Professor	Psychiatry	University of North Carolina, Chapel Hill
2014-2019	Executive Director Rudy Professor	Kinsey Institute Biology	Indiana University, Bloomington
2019- Present	Distinguished University Research Scientist	Kinsey Institute	Indiana University, Bloomington
2021- Present	Professor	Psychology	University of Virginia Charlottesville

29.3 Scientific Impact and Key Contributions to the Field of Behavioral Neuroendocrinology.

Quantitative metrics of scientific impact demonstrate Carter’s broad influence. She has published over 400 articles and chapters and edited five books. Her papers have been cited nearly 33,000 times and her h-index is 90 (Google Scholar, January 2022). While these metrics place Carter in the highest echelon of scientists, they do not adequately capture the three areas in which she is likely to have the greatest lasting impact on the field of behavioral endocrinology:

(1) establishing prairie voles as models to study hormonal regulation of social bonding, (2) catalyzing the study of oxytocin as a behaviorally active hormone in a wide array of species, including humans, and (3) enticing trainees, clinicians and scientists in other fields to incorporate hormonal measures into their behavioral studies.

Carter popularized prairie voles as a wild rodent that could be bred and studied easily in the laboratory. Prior to Carter's first paper on the effects of ovarian hormones on sexual and social behaviors in prairie voles published in 1979 (Dluzen & Carter, 1979), there were only four papers identified by PubMed using the key words "prairie vole behavior" (compared to 653 papers in January 2022). The second crucial step in establishing prairie voles as a model of social monogamy was developing a reliable index of social bonding; in 1992 Carter, Jessie Williams (Carter's post-doctoral fellow) and undergraduate student Kenneth Catania (now a neurobiologist at Vanderbilt University who received a MacArthur Award in 2006 and was named a Guggenheim Fellow in 2014) designed a three chamber testing paradigm, that allowed rapid assessment of preference for the experimental animal's partner versus an unfamiliar vole (Williams et al., 1992). The first paper using this behavioral test established that female prairie voles developed partner preferences more rapidly if they had mated with their partner, but that sex was not required. The behavioral task remains widely used and has been indispensable in identifying the hormonal mediators and neural circuitry underlying social bond formation. To date more than 225 papers have been published on pair bonding in prairie voles.

Carter can also be credited with catalyzing the study of oxytocin as a behaviorally active hormone. In the late 1980's when Carter became interested in oxytocin's potential role in monogamy, it had been extensively studied in the context of uterine contractions and milk let-down. Barry Keverne's group at this time was studying mother-infant interactions in sheep, and published a series of studies indicating that stimulation of the cervix during birth caused the release of oxytocin which in turn was crucial for the onset of maternal behavior, including the formation of a mother-infant bond (summarized in Keverne & Kendrick, 1994). Witt and Carter (1990) demonstrated for the first time that administration of oxytocin altered social behavior between adult prairie voles (Witt et al., 1990). More than 200 papers have subsequently been published on oxytocin and prairie voles and approximately 25% of these papers list Carter as an author. Furthermore, more than 2600 papers have been published on the broad topic of oxytocin and social behavior.

Based on the very similar structures of oxytocin and vasopressin and their intriguing physiological relationship, Carter began studying the role of vasopressin in social bonding in prairie voles, as well. A collaboration between Carter's lab and Thomas Insel's lab at NIMH, resulted in a *Nature* paper demonstrating that ICV vasopressin administration facilitates partner preferences in prairie voles (Winslow et al., 1993). Following publication of this report, there was a sharp increase in papers on vasopressin and social behavior; to date there are more than 1100 papers on this topic.

Carter's influence on the field of behavioral endocrinology is further amplified through the training of dozens of individuals across five decades, ranging from undergraduate research assistants to colleagues in other fields. Carter was an exemplary mentor; her passion for scientific discovery was infectious and being part of her laboratory was exhilarating. She equipped her trainees with the skills needed to develop independence by providing support and guidance without micromanaging projects. She encouraged trainees to think broadly and to take

risks on projects that had the potential to challenge entrenched scientific ideas. Furthermore, she was thrilled when trainees chose to continue studying oxytocin or vasopressin, pair bonding or prairie voles after leaving her lab; there was no mentor-trainee competitiveness. Carter also was a positive role model for aspiring women faculty; she contended, and perhaps more importantly demonstrated, that it was possible to integrate a healthy family life and successful scientific career. Indeed, Carter was celebrating and finding ways to accommodate her trainees' growing families long before universities started talking about policies to support work-life integration.

Carter trained more than 30 graduate students and post-doctoral fellows who have remained in academia or joined NIH or NSF. Among Carter's trainees who joined federal funding agencies that support behavioral endocrinology research are Diane Witt who recently retired after nearly three decades of advocating for neuroscience as a program officer at NSF, Susan Taymans who has been Program Director for the Fertility and Infertility program at NIH for more than 20 years, Luci Roberts who has served several positions in scientific review at NIH, and most recently was appointed to the position of Program Officer in the Behavioral and Systems Neuroscience Branch within the National Institute Aging, and Kristen Kramer, who has several responsibilities within the NIH Center for Scientific Review, including as a Scientific Review Officer in the Emerging Technologies and Training in Neurosciences Integrated Review Group (IRG) and in the Brain Disorders and Clinical Neurosciences IRG.

Zuoxin Wang (Florida State University) is among the dozens of Carter trainees who are still active in behavioral endocrinology research. He was a post-doctoral fellow with Carter; his prolific research program examines dopamine interactions with oxytocin and vasopressin in the regulation of pair bonding in prairie voles, and he uses the model to understand social influence on drug abuse. Laura Redwine studied inflammatory responses to stress among post-partum women as a postdoctoral fellow with Carter (e.g. Redwine et al., 2001) and is currently an Associate Professor of Behavioral and Community Sciences at the University of South Florida studying the cognitive and affective consequences of inflammation. Karen Bales (University of California, Davis), a post-doctoral researcher who studied developmental effects of oxytocin and vasopressin with Carter (e.g. Bales et al., 2003), is a primatologist and leader of the Neuroscience and Behavior Unit at the California National Primate Research Center. She studies the physiology, neurobiology and development of social bonding in prairie voles and titi monkeys (*Callicebus cupreus*), a primate species that forms pair-bonds and males routinely provide care for infants. Bruce Cushing, Chair of Biology at University of Texas El Paso, was a postdoctoral fellow with Carter, and continues to work on the neurobiology of social behavior in prairie voles (e.g. Cushing et al., 2003). Angela Grippo was a postdoctoral fellow with Carter who studied social influences on autonomic regulation of the heart (Grippo et al., 2007); Grippo is currently a Professor of Neuroscience and Behavior at Northern Illinois University and continues to use prairie voles to study the effects of pair bond disruption and social isolation on the brain and behavior. As both a predoctoral trainee and postdoctoral fellow with Carter, Leah Rubin studied oxytocin dysregulation among individuals with schizophrenia (Rubin et al., 2010); Rubin is currently an Associate Professor of Neurology at John Hopkins University studying the influence of various hormones on the cognitive and mental health of women, including those with psychiatric disorders and HIV. Allison Perkeybile was a postdoctoral fellow with Carter studying epigenetic influences on the oxytocin receptor (e.g. Perkeybile et al., 2019) and is currently a Research Assistant Professor at the University of Virginia.

Courtney DeVries, Professor of Medicine at West Virginia University, was a graduate student with Carter studying sexually dimorphic influences of stress on partner preference in

prairie voles (DeVries et al., 1995); she currently studies the influence of social factors on recovery from neurodegenerative disorders and cancer. Adam Perry was a graduate student with Carter (and Cushing) studying neuroendocrine regulation of sociosexual behavior in prairie voles (Perry et al., 2015). He has continued this research as an associate professor at the University of Texas, El Paso. Lindsey Garfield trained with Carter as a graduate student, studying the relationship between oxytocin and depression in low-income women (Garfield et al., 2015); she is currently a faculty member at Loyola University, Chicago. Elise Erickson was a graduate student working with Carter to clarify the relationship between maternal oxytocin and vasopressin concentrations and infant outcomes (e.g. Erickson et al., 2020); she is currently an Assistant Professor of Nursing at the Oregon Health Science Center. William Kenkel was a graduate student with Carter working on the developmental consequences of oxytocin (Kenkel et al., 2019). He is currently an Assistant Professor at the University of Delaware who continues to study the developmental consequences of exposure to oxytocin and vasopressin during the sensitive period around birth.

Carter also participated heavily in training and mentoring of clinician scientists. Suma Jacob (MD, PhD) was a mentored K23 fellow working with Carter on neuropeptide pathways in autism (Jacob et al., 2007) and is currently a Professor of Psychiatry at the University of Minnesota. Carter also helped train Margaret Altemus (MD), an NIH based psychiatrist, who worked with her on postpartum depression and the stress reducing effects of lactation (e.g. Altemus et al., 2005). Altemus is a clinical neuroendocrinologist specializing in Women's Health and an Associate Professor at Yale University School of Medicine. Morris Goldman (MD), a psychiatrist now at Northwestern University worked with Carter to conduct one of the first studies of the benefits of oxytocin in treating the symptoms of schizophrenia (e.g. Goldman et al., 2008). Suen Massey (MD) was a mentored NIH K23 awardee who worked with Carter on postpartum depression and is currently an Associate Professor in Psychiatry at Northwestern University. Brian Kirkpatrick (MD), worked with Carter on prairie vole neurobiology; Kirkpatrick is currently Chair of Psychiatry at the University of Nevada, Reno. James Harris (MD), a child psychiatrist from John Hopkins University, who studied the role of oxytocin in development and meditation with Carter (e.g. Kirkpatrick et al., 1994). Thomas Insel (MD), is a psychiatrist, who Carter introduced to prairie voles as a model for studying social behavior (e.g. Williams et al., 1992); they collaborated on projects for approximately a decade and Insel later became Director of the Yerkes Primate Center and after that was Director of the National Institute of Mental Health at NIH. Carter continues to mentor the training of scientists from other fields including most recently Jessica Connelly (epigenetics, University of Virginia; e.g. Bell et al., 2015), Marcy Kingsbury (developmental neurobiology, Harvard University; e.g. Carter et al., 2020) and Evan MacLean (anthropology, University of Arizona; e.g. MacLean et al., 2017). There are many other accomplished scientists who trained or collaborated with Carter but are not mentioned here because their recent contributions have been in fields other than behavioral endocrinology.

29.4 A Family of Accomplished Academicians and Professionals

Carter met her husband, Stephen W. Porges, at Michigan State where he was completing a PhD in Psychology and she was beginning a post-doctoral fellowship. Porges went on to become the leading expert in the physiological control of heart rate variability and associated behavioral consequences. Of note, he proposed the Polyvagal Theory, helping to redefine the relationship between the evolution of the autonomic nervous system and social behavior in

mammalian species, and how physiological perturbations could elicit behavioral changes and psychiatric disorders (Porges, 1995).

Although Carter and Porges shared scientific interests and often discussed each other's data, they maintained separate careers, publishing together only a handful of times and mostly in the past two decades. Porges is a Professor Emeritus at the University of Maryland and University of Illinois at Chicago, and a Distinguished University Scientist at Indiana University and Professor of Psychiatry at the University of North Carolina. Carter and Porges are a rare example of a two-career academic couple, who were fortunate to land independent faculty positions at the same institutions throughout their careers.

Carter and Porges raised two sons who have likewise established themselves in professional careers. Eric Porges earned a PhD in Psychology at the University of Chicago and is an Assistant Professor in the Department of Clinical and Health Psychology at the University of Florida. He studies the neurobiology of cognitive development across the life span, with an emphasis on the consequences of neural damage caused by HIV and alcohol use disorder. His younger brother, Seth Porges, received his BS and MS in Journalism from Northwestern University and is a freelance scientific writer who also directs and produces documentaries. He is widely published and his documentaries, including *Class Action Park* on HBOmax, have won awards at several film festivals.

29.5 Conclusion.

C. Sue Carter has led an extraordinary life and career as a scientist and mentor. She grew up in a large family in rural Missouri and raised cattle to pay her college tuition. She was broadly trained, earning a BA in Biology from Drury College and a PhD in Zoology from the University of Arkansas, and then undertook post-doctoral training in behavioral endocrinology with Clemens at Michigan State University. Over the subsequent five decades Carter made several key discoveries in behavioral neuroendocrinology, including delineating the roles of oxytocin, vasopressin, and corticosteroids in the regulation of social bonds, biparental behavior, and alloparental behavior in prairie voles, demonstrating the stress-buffering effects of lactation and pro-social behavior, and providing evidence of the importance of oxytocin in promoting human social behavior. Carter held professorships at six universities across her career, including the University of Illinois (Champaign) University of Maryland (College Park), University of Illinois (Chicago), University of North Carolina (Chapel Hill) and Indiana University (Bloomington) and University of Virginia (Charlottesville). She also served five years as Director of the Kinsey Institute at Indiana University. This wide range of experiences provided Carter with unique perspectives that enriched her research program. Lastly, one of Carter's most enduring legacies is likely to be that she was an exceptional mentor to dozens of trainees and colleagues, many of whom were women and individuals from groups underrepresented in science and academia.

Acknowledgements. I thank Sue for sharing 50 years worth of stories and insights with me. It was wonderful to be reminded of the many personal stories behind the scientific discoveries. Unfortunately for the reader I only had enough space to share a small fraction of them here.

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