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PERSPECTIVE



## Marla Sokolowski: and now for someone completely different

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### ABSTRACT

A comprehensive science, technology, engineering, and mathematics (STEM) education has persistent formative effects on individuals, communities, and society. In this regard, Marla Sokolowski's academic legacy will forever reflect her unique contributions to STEM education and mentoring. Furthermore, her creative and multidisciplinary approach to research has resulted in groundbreaking advances in our understanding of behavior genetics. Illustrated here are a few of our life-long learning experiences drawn mainly from earlier parts of Marla's career.

### ARTICLE HISTORY

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### KEYWORDS

Marla Sokolowski; behavior genetics; *Drosophila melanogaster*; foraging

### An emergent behavior geneticist and paradigm

Have you ever offered or contributed to an undergraduate course in which students are required to address a scientific problem, develop a testable hypothesis, establish a plan of execution, collect, and analyze data, consider whether it supports the hypothesis, and write up a cohesive and compelling document? Now imagine that a student comes up with a truly brilliant idea, follows it through with meticulous hard work, and obtains results that are solid enough to publish, form the basis of a Ph.D. project, and become the foundation of an extraordinary and impactful scientific career. That one student was Marla Sokolowski.

During the mid-1970s, Marla Berger (now Sokolowski) – a curious undergraduate then in the Department Zoology at the University of Toronto – was tasked with a laboratory research project in Ellie Rapport's (now E. Larsen, Professor Emeritus) Developmental Genetics course. For this project, she contemplated a comparison of two genetically manipulated strains of flies with obvious differences in morphology. The physical differences were easily explainable... an enzyme here, some pigment there, an extra tuft of bristles where only a few normally sprouted. Beyond these visible phenotypes, Marla found a more compelling challenge in understanding the biological and environmental factors that influenced how the flies *behaved*.

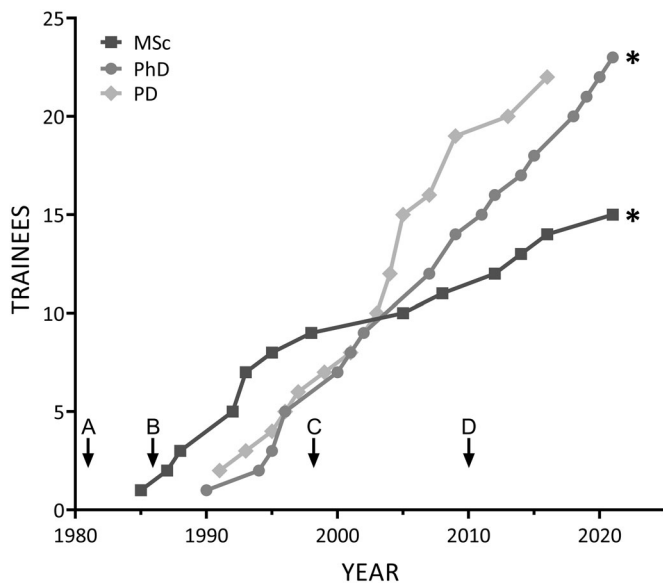
Through discerning observation and careful measurement, Marla described variability in larval movement patterns and devised elegant methods to unravel how and why these differences existed. Meticulous experimental controls and data-driven conclusions were key, especially when teasing apart the multiple factors underlying complex behavior. Marla's work grew and morphed into a Ph.D. project within an energized and eclectic community of graduate trainees

possessing strong evolutionary and mathematical insights (e.g. Jonathan Wong, Clement Kent, and Laurence Packer – her future colleagues), and under the nurturing eye of her Ph.D. advisor (now Professor Emeritus) Roger Hansell.

Marla's analyses of *Drosophila* pre-imaginal behavior set the stage for her transformative career in science and STEM education. As a precocious female principal investigator asking non-traditional scientific questions while immersed in a traditional, male-dominant academic environment at York University in Toronto, there were some inevitable bumps in the road. Notwithstanding, Marla was resolute yet collegial, distinguishing herself by establishing an impactful multidisciplinary approach to research that included the training of dozens of successful scientists of all demographic descriptions (see Figure 1) as well as exposing undergraduates to the truly alluring aspects of animal behavior (and related subjects) through engaging didactic learning. Decades ahead of her time, Marla was indeed different and stood out.

### A multidisciplinary understanding of how and why genes and environment influence complex behavior

The Sokolowski lab has always embodied interdisciplinary science, with research focused on eco-evo-behavioral genetics and behavior assessment of 'pleiotropic' and 'polygenic' traits. Geneticists, field behavioral ecologists, electrophysiologists, statisticians, molecular biologists, and computational scientists co-mingled, collaborated, and co-discovered together (Figure 2 shows some of the earlier alumni). Marla's scientific journey integrated influences from many local as well as international colleagues and collaborators (e.g. Harold Atwood, Yves Carton, Ralph Greenspan, Jeff Hall, Ulrike Heberlein, Art Hilliker, Jerry Hirsh, Jean-Marc Jallon,



**Figure 1.** Marla Sokolowski mentoring and faculty appointment timeline. The cumulative number of completed Master's (squares), Doctoral (circles) theses and hosted Post-Doctoral Fellows (diamonds) are shown. \*In progress. Appointments: (A) NSERC (Canada) Postdoctoral Fellow York University. (B) Tenure-track Professor, York University. (C) Professor, University of Toronto (Mississauga). (D) Professor, University of Toronto (Main Campus). In addition to *Drosophila* behavior genetics, Marla has supervised research on guppies (A–B), lekking grouse (B–D), honeybees, locusts, and ants (C–D), and currently with mice and humans (D).

Tadeusz Kawecki, Bambos Kyriacou, Joel Levine, Trudy MacKay, Frederic Mery, Catherine Rankin, John Ringo, Gene Robinson, Roland Strauss, Tim Tully, Louise Vet, Doug Wahlsten, and others). This created an energized and colorful environment, buzzing with graduate and undergraduate students, postdocs, and visiting academics. Although *Drosophila* was the primary model organism in the 1980s and 1990s, analysis of behavioral phenotypes extended beyond larval foraging. Marla supervised Doctoral projects using other systems such as social behavior in guppies and mating behavior in lekking grouse (Figure 1). These programs added a dimension of scientific understanding in her group that was rarely found in a single laboratory at the time.

By promoting the scientific process to study behavior, genetics training in the Sokolowski lab provided lessons that transformed learning and teaching (Figure 3). The *Drosophila* model permits controlled investigations of behavior in ways that are not possible with other systems and especially not in humans, such as the exchange of different genetic backgrounds to test for phenotypic effects of variation at a single locus. Furthermore, the ability to control and manipulate fly genes (including genetic background) and environment (developmentally and experimentally) enable precise interrogation of gene-environment interactions. This informed Marla's translation of relatively 'simple' larval behavior toward a better understanding of behavioral paradigms across models, phenotypes, and in biomedical research. Through decades of collaborative and multidisciplinary science that included neurogenetics, genomics, and epigenetics, her integration of model species and behaviors extended to locusts, bees, ants, mice, and humans (Figure 1).

## An engaging educator, empowering mentor, and inspiring model scientist

Marla has had a remarkable impact on STEM education throughout her career. Her unique undergraduate courses evaluated students on their application of knowledge to resolve novel research problems using critical thought and the scientific method, acquired through Socratic instruction. By promoting the importance of effectively translating science in society, her teaching and research impart a progressive view in historical context, enabling discussions of topics such as the roles of genes and environment, particularly as they apply to humans. Notably, her appreciation of genetics and evolution allows for a deep understanding of how errors and misconceptions can have harmful social consequences.

*Drosophila melanogaster* is the ideal model system for hands-on genetics instruction, easily permitting young researchers to initiate research in a laboratory setting. Undergraduates from Marla's courses were frequently encouraged to visit the lab and test-drive their basic fly pushing skills. During the 'York' years, students sustained with beer money and bus fare stipends were often introduced to research with summer fly projects. Since the *Drosophila* larval pathlength assay required many hands working together, trainees also had the opportunity to 'get their fingers wet' in collaborative research. The Sokolowski lab always incentivized inclusivity, where the scientific process was knitted together by each one's experiences in conducting research as well as developing critical thinking and communication skills. As in many well-oiled scientific machines, this stimulating social environment enabled by Marla was creative, productive, and great fun. Unfortunately, and for the sake of simplicity, many legendary stories have been necessarily omitted from this tribute to our former leader.

Marla's mentoring and teaching styles, taken together with her provision of research opportunities, continuously promoted retention of science students – regardless of gender, sexual orientation, culture, religious belief, or skin melanin content. Open discussions of career paths were encouraged among all those interested, engendering a sense of belonging in a field that students may have traditionally considered their involvement to be non-normative. Students in the lab who began as undergraduates, and who demonstrated a capacity and passion for the work, were encouraged to consider graduate school. A sense of belonging and of helping develop the scientific process was supported by an inclusive, collaborative environment among all – undergraduates, graduate students, and post-docs.

## Building effective, rewarding, and socially relevant professional careers

Beyond undergraduate teaching, Marla's collaborative and interdisciplinary style of research and mentoring were critical to establishing a forward-looking graduate training program that prepares students for effective professional scientific careers. She herself is an unwavering example of effective communication, collegiality, and collaboration.



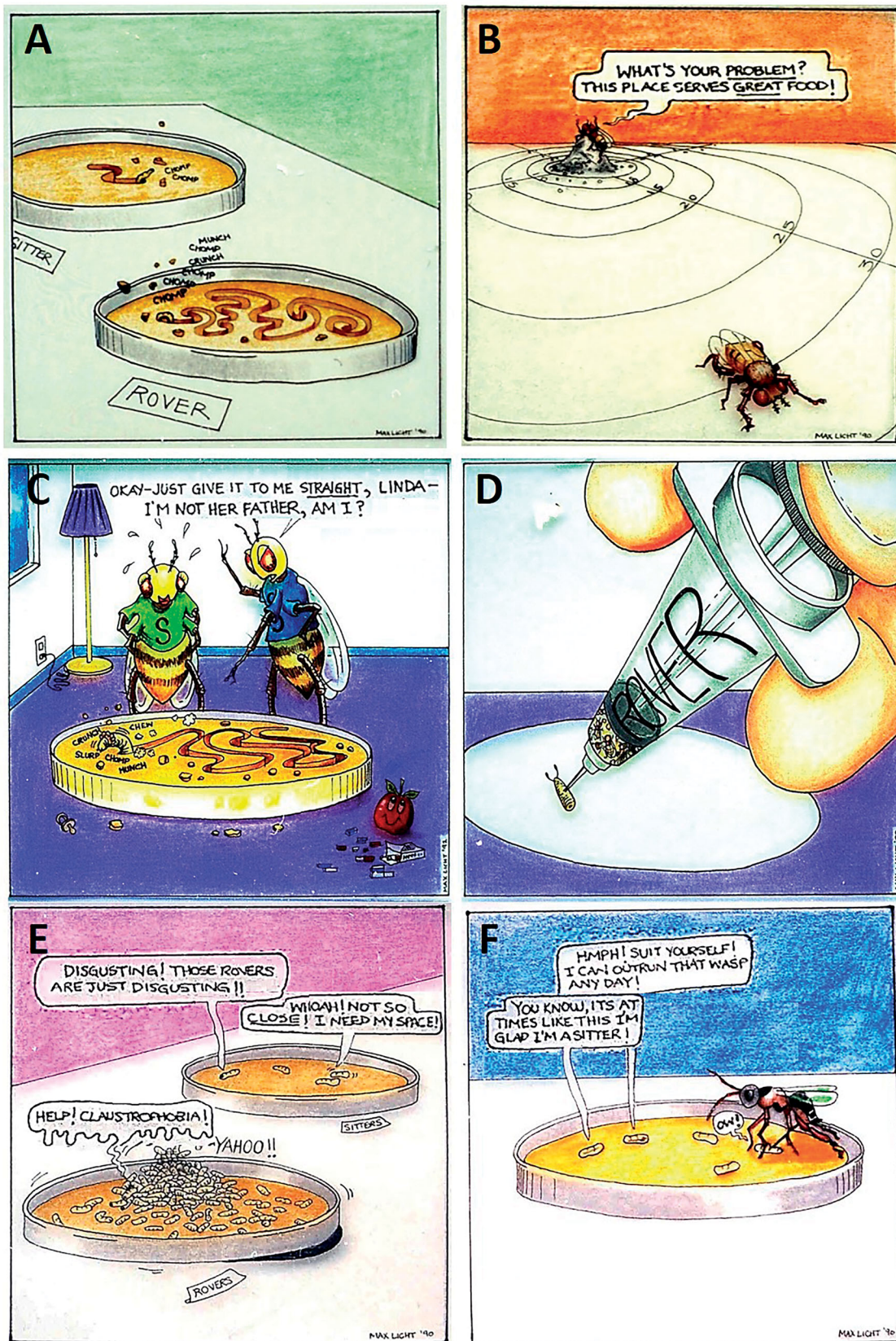


**Figure 2.** Sokolowski lab alumni (1982–2002). (A) Marla and Yehuda Ben Shahr, *Drosophila* Neurobiology Course, Cold Spring Harbor Laboratory (CSHL), Cold Spring Harbor, NY, USA (June 2002). (B) Marla, University of Toronto, Toronto, ON, Canada (ca. November 2020). (C) Marla and Steven de Belle, York University, Toronto, ON, Canada (June 1987). (D) Craig Riedl, *Drosophila* Neurobiology Course, CSHL (July 2001). (E) Lucy Rodriguez, York University (June 1988). (F) Larval foraging assay demonstrated at the *Drosophila* Neurobiology Course, CSHL (June 2002). (L–R) Christine Serway, Marla, Amsale Belay, Josh Krupp, Xuecai Ge and Michelle Steinhilb. (G) Marla, York University (ca. 2001). (H) (L–R) Lionel Peypelut, Craig Riedl, Susan Shaver and Karen Williams, 37th Annual *Drosophila* Research Conference, San Diego, CA, USA (April 1996). (I) Sharon Bauer and Marla, Behavior Genetics Association Annual Meeting, Bloomington, IN, USA (June 1984). (J) Sokolowski–Hilliker Lab Picnic, Glenn Eden, ON, Canada (July 1990). Front (L–R) Sofia Pereira, Stephanie Butland, Helen Rodd. Middle (L–R) Denise Michaud, Marla, Tony Parkes, Kim Hughes, Leonard Tsuji, Pino (undergraduate), Daniel Eberl. Back (L–R) Art Hilliker, Paul (friend).

Tenure in Marla's research group has been inspirational for every trainee she has touched, leading many to follow in her footsteps. The scientific journey for some alumni began as students in Marla's undergraduate courses, with the often-startling realization that graduate school and a future in science was even possible. The benefits of Marla's mentoring approach and shared collaborative experiences shaped her students and their professional choices, resulting in effective teaching, training, and research strategies in many of their future classrooms and laboratories. That numerous alumni are currently engaged in productive scientific careers is a noteworthy measure of Marla's mentoring and academic inclusive fitness.

Science in society is meaningless without effective communication, a lesson transmitted through Marla's insistence that lab members develop skills and strategies for discussing their work. This is aided by regular lab meetings in which everyone is included and incentivized to participate. She builds confidence in those with anxiety about speaking in public – often through sharing stories of her own initial fear of speaking, along with her (always amusing) resolutions of the problem. Empowered and practiced, students eventually develop their own skills, take on more difficult public speaking challenges and quickly experience the satisfaction of sharing their excitement about science with others. Most of Marla's graduate students have at least one terrifying story





**Figure 3.** *Drosophila* behavior genetics. Experiments and lessons learned in the Sokolowski lab, as illustrated by Max Licht (ca. 1990–1992). (A, B) Foraging behavior assays showing Rover and sitter differences in pathlength phenotypes of larvae (A) and adults (B). (C, D) Rover is genetically dominant to sitter, explaining the difficult conversation for these sitter parents of Rover  $F_1$  progeny (C), and how germline transformation of sitter ( $for^S$ ) embryos with Rover ( $for^R$ ) cDNA will generate Rover progeny (D). (E, F) Maintenance of the Rover/sitter genetic polymorphism by density-dependent selection (E) and parasitoid wasp-dependent selection (F).

of a conference presentation or of an appointment to speak with a revered scientist – to later realize how much was learned from the experience. Although a successful outcome cannot be guaranteed, it is more likely when enabled by a strategic and supportive mentor like Marla.

Dedicated to empowering scientific autonomy to her trainees, Marla works tirelessly and patiently to ensure that every student-authored document is well organized to convey a carefully crafted message. Rather than writing presentations, papers, and grant applications herself, she endlessly reviews and gently incentivizes each student to develop their own concise and clear scientific language. This colossal investment has resulted in an impressive 162 peer-reviewed publications (as of October 2020). Besides manuscripts and presentations, scientific communication is further encouraged by another student-focused strategy worth noting. When one of Marla's many scientific colleagues visits the lab, they are never sequestered in her office during their stay. Instead, they are introduced to lab members individually or in small groups. Thus, each trainee receives the benefit of an engaged scientific discussion with an expert in some area of research relevant to theirs. The immediate benefits of this practice are obvious: experiences in communicating ideas with leading scientists, the gain of specific advice about experiments, as well as bigger picture perspectives on scientific thought. In the long term, this personalized exposure translates to more creative and impactful research strategies, trainee integration within the scientific community, and the establishment of contacts that facilitate opportunities for career development after graduation.

### **A few final words about the authors and about Marla**

The authors are Sokolowski lab alumni with active careers in research, STEM education, healthcare, biotech business,

and industry. Their work in *Drosophila* with Marla included: Sofia, mating behavior (undergraduate, 1990), analysis of adult foraging behavior and genetic mapping of the *Chaser* gene (Ph.D., 1995); Karen, diapause genetics (M.Sc., 1992; Ph.D., 2001), currently working on phenotypic plasticity and behavior; Steven, genetics of foraging behavior (M.Sc., 1987) and characterization of the *foraging* gene (Ph.D., 1990). The authors have contributed to 15 peer-reviewed manuscripts with Marla.

While working on this piece, we met regularly, reminisced fondly about our time with Marla, and caught up on her extraordinary scientific journey. We quickly realized that it would not be possible to fully portray Marla as the person and the scientist with a career spanning over four decades, or our many colorful experiences with her, in a few pages. To place the significance of her contributions in perspective, we are thrilled that Marla is the 2020 recipient of the Royal Society of Canada's (RSC) Flavelle Medal for meritorious achievement in the biological sciences (<https://www.artsci.utoronto.ca/news/university-professor-marla-sokolowski-receives-royal-society-canadas-flavelle-medal-her>). She is only the second woman to be so decorated since the award was established in 1924. Marla both exemplifies and promotes diversity, inclusivity, and life balance in building capacity for scientific discovery. She is truly someone completely different.

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### **Disclosure statement**

No potential conflict of interest was reported by the author(s).