

In Memoriam: Barry Sinervo 1961–2021

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In March 2021, evolutionary biologist and ecologist Professor Barry Sinervo at University of California Santa Cruz (UCSC) passed away at the age of 60, after a brave struggle with cancer (Fig. 1). Barry is mourned by his wife of 32 years Jeanie Vogelzang, his son Ari Sinervo, and other family members. His premature death has also caused much sorrow among his departmental colleagues at UCSC, scientific collaborators around the world, and former students and postdocs, including the authors of the current piece. Here, we summarize Barry's scientific achievements, discuss his legacy, and provide some personal memories of our interactions with him when carrying out research in his laboratory. Those of us writing this article are former postdocs and PhD students who all spent considerable time in Barry's laboratory, and we wish to share some of the intellectual excitement we experienced during these formative years of our academic careers. Together, our team covers a large time span of Barry's faculty career, and the authors of this piece include Barry's first PhD student (R.C.), his first European postdoc (E.I.S), his last PhD student (P.B.) as well as his co-workers, students, and laboratory members in between these periods (A.M.A., L.L., and S.C.M.), from 1997 and onwards.

Barry started his scientific career by earning a B.Sc. in biology and mathematics at Dalhousie University in Nova Scotia. He then joined the Department of Zoology at Washington University, under the supervision of Professor Raymond Huey. It was during these early formative years that Barry developed the classical experimental protocols that would subsequently establish him as a

young and rising star in evolutionary biology: experimental techniques to manipulate egg and offspring size, that he termed "allometric engineering." By experimentally removing part of the yolk from eggs of two species of sea urchins (*Strongylocentrotus*) and later also Western Fence Lizards (*Scleroporos occidentalis*) and side-blotched lizards (*Uta stansburiana*), Barry and his colleagues explored the fitness and performance consequences of maternal effects and early developmental history on offspring (Fig. 1B). This pioneering experimental work resulted in a series of classic and highly influential papers published in *Evolution* and *Science* (Sinervo and McEdward 1988; Sinervo 1990; Sinervo and Huey 1990; Sinervo et al. 1992). Barry's early work illustrates his interest in both development and ecology, and how a knowledge of both fields is crucial to understand evolution. Barry was an early pioneer in linking ecology to development and evolution, well before the later rapid growth of evolutionary developmental biology ("evo-devo") as an emerging and increasingly popular research topic. Barry's experimental manipulations of offspring size revealed the mechanistic links between size and offspring performance, including how ecologically important traits like sprint speed are important for lizards to escape predators and the general importance of allometric size-performance relationships. These classical experimental phenotypic manipulations also revealed the importance of early environmental effects and offspring development, which many biologists nowadays appreciate as being fundamental to understand both ecological and evolutionary dynamics of natural populations. It provided the

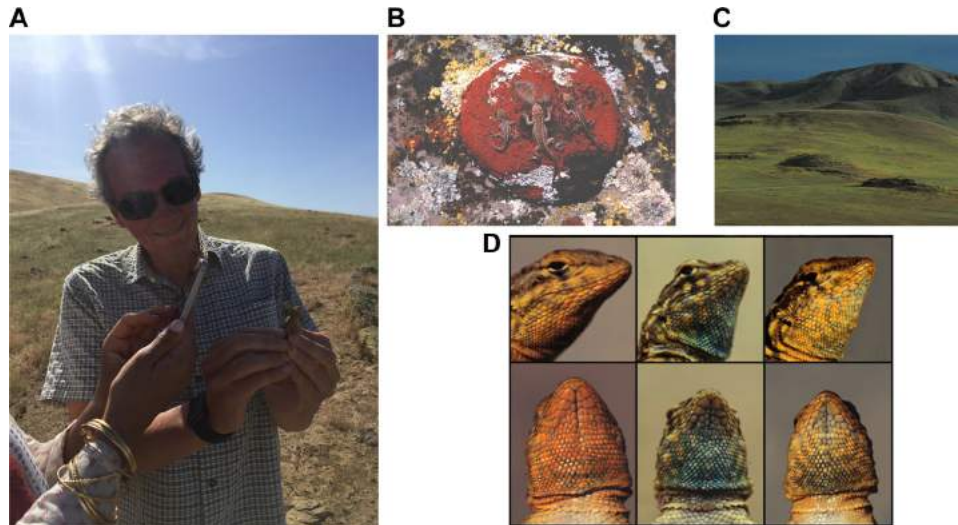


Figure 1. Overview of the research achievements and scientific career of Professor Barry Sinervo, who passed away at the age of 60 in March 2021. (A) Barry in his natural habitat at his study site; catching and processing side-blotched lizards (*Uta stansburiana*) at Los Baños, Merced County (CA, USA). Photo by Pauline Blaimont. (B) Hatchling side-blotched lizards that have been subject to experimental manipulations, using the techniques of “allometric engineering” that Barry developed during his PhD student and postdoc periods. Left: miniaturized hatchling, emerging from an egg where part of the yolk has been removed. Middle: gigantized hatchling, emerging from a follicle-ablation experiment on adult egg-bearing mother. Right: unmanipulated “control” hatchling, emerging from an unmanipulated egg. Photo by Barry Sinervo. (C) The semi-isolated rocky outcroppings at the field site at Los Baños, where Barry’s long-term study of marked individuals and natural selection in the wild took place. Photo by Barry Sinervo. (D) The three male color morphs in the side-blotched lizards, described by Barry and Curtis Lively as a “Rock-paper-scissor game” in 1996. Left: orange-throated males. Middle: blue-throated males. Right: yellow-throated males. Photo by Barry Sinervo.

foundation that established him as a truly integrative evolutionary biologist. This work also earned him the Society for the Study of Evolution’s (SSE) *Theodosius Dobzhansky Prize* in 1992, and a *Young Investigator Award* from the American Society of Naturalists. Interestingly, Barry’s advisor Ray Huey did not believe that these experimental manipulations would work and advised him against doing them, but he was happy to be proven wrong when they turned out successful (R. Huey, pers. commun.). This episode underscores that PhD students should not always follow the advice of senior supervisors and that pushing through ideas you really believe in can lead to scientific innovations.

After defending his PhD in Seattle, Barry subsequently moved to UC Berkeley, where he obtained the prestigious Miller postdoctoral fellowship, working with the endocrinologist Professor Paul Licht. During this time in Berkeley, Barry developed his interests in the mechanistic and developmental basis of life-history variation. He designed experimental endocrinological manipulations on female side-blotched lizards with the aim of understanding the trade-off between egg quantity and egg quality. By experimentally manipulating circulating levels of follicle-stimulating hormone (FSH) in females, he showed in a paper in *Journal of Experimental Zoology* that this hormone had pleiotropic effects on both traits: it simultaneously increased egg number and decreased egg size as a correlated effect (Sinervo

and Licht 1991a). This was a groundbreaking experiment that resulted in a paper in *Science* (Sinervo and Licht 1991b) and which established a concrete and mechanistic proof-of-principle of the theory that life-history trade-offs were likely to emerge as a result of antagonistic pleiotropy of genes with effects on several different traits, as discussed in a later publication by Barry in *American Naturalist* (Sinervo 1999).

After obtaining faculty positions as professor, first in Bloomington at Indiana University and subsequently at UCSC, Barry continued to study side-blotched lizards in an individually marked field population at Los Baños (Merced County) in California (Fig. 1C). He chose this study location after driving around a large part of California, scouting out different sites that would be suitable for a long-term population study of marked individuals. Once Barry had settled on the field site at Los Baños, he continued to use his experimental techniques and applied them in the field, aiming to understand how natural selection shaped life-history evolution in a realistic ecological setting. The landscape at Los Baños is characterized by dry, grassy areas and rolling hills, where enormous numbers of lizards live in high density on semi-isolated rocky outcroppings (Fig. 1C). Although these little animals are fleet of foot (Barry would have called them “wiley”), he had mastered the art of capture and routinely captured and processed more than 100 individuals per day. Those of us who

participated in the field work at Los Baños often participated in daily competition with Barry to catch as many lizards as he did, but he was typically able to catch more than the rest of the team combined during a whole day, which says a lot about his outstanding skills as a field biologist.

It was after several years of field work at Los Baños that Barry discovered and described the evolutionary and social dynamics leading to perhaps his most famous paper in *Nature* in 1996: “The rock-paper-scissors game and the evolution of alternative male strategies” (Sinervo and Lively 1996) (Fig. 1D). Together with his colleague Curtis Lively (still at Indiana University), they described three heritable male throat color morphs that persist in this population, while fluctuating in their relative frequencies every generation (Sinervo and Lively 1996). Based on field data and game theoretical modeling, Barry and Curt argued that this polymorphism was maintained by a particular form of negative frequency-dependent selection (NFDS), namely a rock-paper-scissor game (RPS), in which the different morphs showed intransitive fitnesses, each morph having its own strengths and weaknesses in intrasexual selection and competition over access to females and mating opportunities (Maynard Smith 1996). RPS had previously been a theoretical idea, explored by the evolutionary theorist John Maynard Smith, but here was a possible case of its operation and existence in a natural population in the wild.

It is fair to say that the RPS-paper was met with some skepticism by many evolutionary biologists and the idea does not seem to have had a big impact on the field of behavioral ecology. However, outside of behavioral ecology, intransitive fitnesses in general, and the RPS-paper in particular, have had a huge impact in fields like theoretical evolutionary biology, biodiversity, adaptive radiations, community ecology, evolutionary genetics, and microbial experimental evolution (Rainey and Travisano 1998; Palumbi 1999; Czárán et al. 2002; Kerr et al. 2002; Zhang et al. 2013; Arnold 2020). We strongly suspect one reason why behavioral ecologists have not fully embraced the concept of intransitive fitnesses and the RPS is a cultural barrier: in the behavioral ecology tradition, there is often a strong focus on evolutionary endpoints and optima, rather than on the dynamics of the evolutionary process. To be fair, Barry had a tendency to oversell the RPS, and the dynamical complexity within Barry’s conceptual evolutionary models sometimes became intractable. Barry strongly rejected simpler concepts such as indirect genetic effects (IGE) arising from social and parental interactions (Wolf et al. 2001) that could potentially explain the observed patterns. Barry claimed that these more simplified approaches sacrificed mechanistic insight to tractability at the cost of understanding. This position reflects Barry’s integrative approach, which aimed to merge genetics, development, physiology, and mathematics to understand the evolutionary process. Barry therefore did not shrink from complexity and attempted to understand rather than

minimize its impact. The last words about the RPS and the male color polymorphism have probably not been said, but we strongly suspect that Barry got the major picture right about how this and other forms of enigmatic behavioral polymorphisms are maintained.

In 1998, interested in studying dispersal in the side-blotched lizards, Barry visited Jean Clobert in Paris. Barry and Jean immediately had passionate discussions about how dispersal could be linked with the three color morph system. Barry visited Jean’s captive common lizards at Foljuif (south of Paris) and to Jean’s surprise they discovered that female common lizards also displayed some color morphs. From this first encounter, a long-term collaboration between Barry and Jean was established primarily focused on color morphs, the role of corticosterone, and the effects of climate change. In common with many of us, Jean has data and experiments that he carried out with Barry that are still to be published. Jean treasures Barry’s personality and will forever remember the intense scientific discussions they had over the years. A common theme in all our memories of Barry is that he was certainly one of the rare people with whom we have had such rich scientific exchanges.

Several of us in the group shared Barry’s strong interests in maternal effects, and particularly the idea that maternal physiology could be a powerful way to translate social dynamics into offspring developmental trajectories. This work led to a series of papers on the role of early environmental and maternal effects and the effects on phenotypic integration, including how egg size and maternal hormone investment can trigger changes in phenotype to successfully integrate each mating type with effective antipredator strategies (Lancaster et al. 2007, 2010; Paranjpe et al. 2013). This work was strongly facilitated by Barry’s curiosity-driven research efforts, aiming to link social environments with physiology and with the aim to understand the complexity of dynamic evolutionary processes.

In addition to his papers, Barry also leaves behind a global network of scientists grateful for their time spent interacting with him and others in the vibrant environment he created in his laboratory. The authors of the current piece all spent some of our formative years in Barry’s laboratory. The insights we gained by interacting with Barry and other members of the laboratory were instrumental for us in our subsequent research careers. Below, we include some personal anecdotes to provide a general flavor of the unique and extremely creative research environment that we experienced in Barry’s laboratory.

One of us (E.I.S.) joined Barry’s laboratory as a postdoc at UCSC in 1997, when Barry was a young faculty member (36 years) and had just started his position. E.I.S. was Barry’s first postdoc, and came from Sweden where he had mainly been exposed to classical behavioral ecology during his PhD. It was somewhat of a cultural and scientific shock being exposed to

a new way of thinking in Barry's laboratory, where population genetics, development, and big questions in evolutionary biology were discussed during laboratory meetings and during commutes to the field site at Los Baños. Initially, E.I.S. found himself in doubt over the basic story about the lizard throat color polymorphism and the causes of its evolutionary maintenance, and he was not alone in the laboratory in these feelings. Working with Barry in the field, compiling data and performing experimental investigations gradually convinced E.I.S. that this polymorphism was indeed a real phenomenon in demand of explanation. Together with Barry and several other colleagues in the laboratory, including A.M.A., we also explored the dynamics of the color polymorphism in females, its fitness consequences and genetic background, and documented striking genetic correlations between color, immune function, and life-history traits (Sinervo et al. 2000; Sinervo and Svensson 2002; Svensson et al. 2009).

Another one of us (S.C.M.) met Barry while he was in Finland as the external examiner of a PhD thesis in 2002, was encouraged to apply for funding, and would go on to visit his laboratory every spring for 4 years from 2003 to 2006. One year, together with L.T.L. and Donald Miles, we decided to investigate proximate mechanisms behind the behavioral, physiological, and morphological differences of the different color morphs. In true Barry style, we carried out a natural selection experiment in the field, investigating selection on suites of hormone-mediated traits. Rather than manipulating testosterone (T) and corticosterone, Barry was enthusiastic to look at the upstream gonadotropins luteinizing hormone (LH) and follicle-stimulating hormone (FSH) that regulate T to highlight endocrine cascades. Through manipulations of LH and FSH, whose natural expression is thought to be under genetic control, we also showed that the responses to hormones in the different color morphs were at least partly adaptive. For example, the yellow-throated male morph is more plastic and can upregulate these hormones opportunistically, whereas the other morphs lack such plasticity (Mills et al. 2008). Despite the scale of these projects, the laboratory was a well-oiled machine with lizards in multiple coolers arriving to be processed and then returning to the field. Even when S.C.M. was isolated at home with TB (which Barry diagnosed in 5 minutes though it had baffled doctors for months), the coolers kept on coming, the doorbell would ring and the cooler would be left there on the doorstep!

When P.B. (Barry's last PhD student) told her then herpetology professor, Dr. Jim Archie at Cal State Long Beach that she had been accepted into Barry's laboratory, he dropped everything to give her a huge hug in his excitement for her to enter into the laboratory of one of the greats. Barry's influential RPS work, textbook material in her undergraduate courses, left P.B. feeling slightly intimidated to join a laboratory with such a big name. Although Barry was a big name with big ideas, he had an equally

big heart. Barry lived and breathed for the lizards, so much so that even in the trenches of his fight with cancer and in the worst of the COVID pandemic, to preserve the work and isolate himself he lived in an old trailer on the field site itself so he did not have to make the long drives to and from his home. His dedication was admirable.

Barry certainly never thought small, and it was exciting to be involved in his large ideas. We try to continue this legacy today and encourage our students not to shy away from whole-organismal performance experiments. We also repeat more trivial but amusing day to day quotes from Barry, such as the five Ps: *Prior Planning Prevents Poor Performance*, an important classic as Lizard Land was a couple of hours drive away from the laboratory. Barry also leapt at any occasion to teach, such as the time one of us (S.C.M.) chose a rock to sit on whilst filling in field notes. The rock was hiding a rattlesnake coming out of hibernation which soon let us know of its presence, but unaccustomed to this sound, it took Barry's shout of *RUN!* to get S.C.M. moving. Once scattered field notes had been retrieved and Barry's laughter had subsided, he proceeded with a short, but detailed and interesting description of how that rattle would forever be embedded in her amygdala and hippocampus.

The formative years in Barry's laboratory stimulated our interests in correlational selection (selection for different character combinations), genetic and phenotypic polymorphisms, adaptive landscape theory and its various applications. Our interests in adaptive landscape theory and applications were also partly stimulated by the physical landscape of the dry, rolling grassy hills at Los Baños and "Lizard Land." Indeed, Barry would often wax poetic on the long drives to California's great Central Valley, comparing the rugged landscapes of the Diablo range to Sewall Wright's adaptation heuristic. These long drives were an important resource for all of us, as they provided rare opportunities to gain uninterrupted access to Barry, whose pace of work (both physical and intellectual) were so intense that he was otherwise tough to pin down. We drove to the field site together each day, riding in Barry's filthy 1986 Toyota 4runner. Whoever sat up front with Barry on the ride home had nearly 2 hours of private audience to chat, while the others, exhausted from a long day under the hot Valley sun, would sleep in a pile in the backseat. Barry was just as happy to talk about science and natural history, as he was to recount stories of his metaphysical experiences with a crow in the desert, but in the background, his mind was always turning over the problem of natural selection acting on the lizards with those brightly colored throats. As a result of the vibrant intellectual atmosphere in Barry's laboratory, E.I.S. and R.C. (who was one of Barry's first PhD students) some years later edited a joint volume about adaptive landscapes together (Svensson and Calsbeek 2012). L.T.L. later across the Atlantic to Sweden became a postdoc in the laboratory of E.I.S., eventually

establishing herself as faculty member at University of Aberdeen in the UK.

Barry was half-Finnish and thanks to his mother was fluent in Finnish. In 2004 in Jyväskylä (Finland), Barry astonished the audience, and delighted the Finns, at the 10th Jubilee Congress of the International Society for Behavioral Ecology (ISBE), by starting his plenary in Finnish. One half of the audience was certainly shocked as 5 minutes into his talk, Barry was still speaking in Finnish! Otherwise, Barry was never very fond of going to international conferences but he traveled extensively and had a huge international network of collaborators all over the world. His laboratory was surely an intellectually very stimulating and international arena, where many long-term friendships and close collaborations were initiated, with or without his active involvement. We are very grateful for this indirect influence that Barry had on our research careers and that emerged more or less spontaneously in the stimulating but also challenging environment that his laboratory constituted with many brilliant and creative minds flourishing and joining from different parts of North America, Europe, and many other parts of the world. E.I.S. and L.T.L. also remember being introduced by Barry to some classics in evolutionary biology, such as William Provine (1971), Richard Levins (1968), and Richard Lewontin, in particular *The Dialectical Biologist* (Levins and Lewontin 1985). Barry had a remarkable breadth of knowledge in the history of ecology and evolutionary biology, including philosophy and dialectical thinking. This knowledge base clearly influenced the way he thought about science, carried out his research, and supervised his students and postdocs.

During the last part of Barry's career, from 2008 and until his premature death in March 2021, his research efforts were mainly directed toward problems of ongoing climate change and its potentially disastrous consequences in terms of increased extinction risks of animal populations. Barry and a large team of collaborators from all over the world published a highly cited paper in *Science* in 2010, where they highlighted and described the risks of altered thermal niches and elevated extinction risks of lizards in the face of rapid climate change and global warming (Sinervo et al. 2010). Barry also co-authored another influential study documenting the collapse of desert bird communities in the Californian Sonoran desert, which was also attributed to climate change (Riddell et al. 2019). Although the lizard study was later criticized by other researchers who questioned the alarming conclusions that 39% of lizard populations and 20% of species would go extinct by 2080 (Clusella-Trullas and Chown 2011), Barry and his colleagues responded to these criticisms and maintained their pessimistic message (Sinervo et al. 2011). Only time will tell whether Barry and his colleagues were correct, but there are other worrying studies indicating that climate-mediated extinctions might already be happening in taxa other than lizards

(Wiens 2016; Lister and Garcia 2018). Barry's worry and engagement with the threats from climate change were sincere. Whether one agrees or disagrees with his pessimism about a forthcoming and dramatic wave of climate-mediated extinctions of lizards, his family members encourage all those who want to honor Barry's memory and work to donate to the climate movement and organization "350 Org" (<https://350.org/>), which fights for a sustainable future and for a transition to a better future free of fossil fuels.

Finally, it might be worth reflecting about how Barry saw his research on climate-mediated extinction risks being related—if at all—to his earlier work in more basic science in life-history evolution, sexual selection, game theory, and color polymorphisms. We have also asked ourselves this question, and are quite confident that he did not view these lines of research as being separate lines of inquiry, but rather as reflecting his general curiosity in understanding our natural world and life on this fragile planet. His later work on how temperature conditions and early environmental effects interacted with lizard throat colour exemplifies such integrative science, spanning climate change research, sexual selection, and life-history evolution (Paranjpe et al. 2013). Barry was unfortunately unable to complete his research and provide a general summary of his different research themes, but he was thinking deeply about how to apply game theory to accelerate the transition from a world dominated by fossil fuels to a more sustainable future. He was also thinking about how to apply RPS-related ideas to understand the universe at large, plans that he mentioned to E.I.S. in their last physical meeting in Santa Cruz in January 2020. We finish this obituary by noting that there is a growing research interest and attention to how climate change and temperature can affect sexual selection, sexual conflict, and the evolution of color polymorphisms (Lancaster et al. 2017; García-Roa et al. 2020; Svensson et al. 2020). We are sure that Barry would have been delighted and excited by these recent developments.

AUTHOR CONTRIBUTIONS

E.I.S. wrote the first draft of this manuscript based on discussions and with input from all the other co-authors. P.B., R.C., L.T.L., A.M.A., and S.C.M. all contributed to subsequent additions, rewriting, and finalizing of the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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