

Research Background | I began my academic career investigating how sociality drives the evolution of cognition, which in turn, shapes mammalian behavior and ecology. My early work contributed a novel perspective in animal cognition by leading the first formal investigations of cognition in big cats. In a series of experimental studies, I demonstrated that social carnivores outperform asocial ones in tasks requiring problem solving (Borrego & Gaines 2016), provided the first evidence of learning and memory in lions (Borrego & Dowling 2016), and showed that social tolerance fosters cooperation (Borrego 2020). This work expanded comparative cognition to include big cats, a taxon largely absent from the field, and demonstrated their value for testing theories linking social and cognitive complexity. It also generated student-led research, including a master's thesis on innovation and behavioral flexibility in lions and snow leopards that resulted in a peer-reviewed publication (O'Connor, Chase, Chodorow, & Borrego, 2022). The student went on to pursue a PhD, underscoring the potential of this research avenue to cultivate emerging scientists. Together, these early lines of inquiry provided the foundation of my current research trajectory.

Research Program & Approach | Building on this foundation, my current research focuses on lions' behavioral plasticity across ecological contexts (reviewed by Palmer, Borrego & Packer 2023; Borrego, Chakrabarti & Finerty et al., *under revision for Animal Behavior*). Lions' fission–fusion societies, combined with their occupation of ecosystems ranging from deserts to savannahs, forests, and even coastal systems, make them an ideal model for testing classic and emerging theories of cooperation, plasticity, and social–ecological adaptation. At its core, my program addresses three central themes: (1) investigations of sensory ecology, examining how lions navigate their environmental and social landscapes, such as the role of roaring in shaping fission–fusion dynamics; (2) the ecological conditions under which social cohesion and cooperation emerge or break down; and (3) how behavioral plasticity enables animals to adapt across diverse environments, offering clues to how climate change may reshape behavior. To address these questions, I employ a multi-pronged approach. In the field, I combine direct observation with innovative collaborations, including partnerships with San trackers whose unparalleled knowledge enriches behavioral data collection (Borrego & Finerty et al. 2024; Borrego & Finerty et al. *in press African Journal of Wildlife Research*). In parallel, I conduct experimental studies through long-standing zoological partnerships that allow controlled studies of behavior and its cognitive underpinnings.

As one example of how these methods come together, my 2020 study (Borrego & Dowling) found that lions did not show coordination-based cooperation in a controlled task, prompting me to extend this line of research into the field. In the resource-scarce Central Kalahari, my ongoing work shows that lions hunt significantly more frequently as solitaires rather than cooperatively (*in prep*), yet contrary to prevailing explanations of cooperative hunting in lions, solitary hunters still regularly capture large, risky prey such as gemsbok and giraffe; cooperation breaks down in this system. Surprisingly, solitary hunts are also significantly more likely to include nonparticipants feeding at the kill. Whereby, group members that did not participate in energetically costly hunts are nonetheless tolerated at the carcass. These findings raise compelling questions about the conditions under which cooperation is favored or breaks down.

My current work reveals that resource availability is a key piece of the cooperative puzzle. Low resource availability, including limited prey, constrains pride size, often reducing groups to as few as two adult females with dependent offspring. In turn, scarce and unpredictable prey may drive a 'divide and conquer' strategy. Adults split-up to increase efficiency, whereby the first to encounter prey makes the kill, with the delayed benefit that roles may reverse in future hunts. Alternatively, one female may remain behind with dependent offspring while the other hunts. These dynamics highlight how ecological constraints and social roles intersect to shape cooperative strategies (*ongoing research*). Cooperative hunting provides one illustrative case of these dynamics, but it represents only one facet of a broader program examining how behavior adapts to ecological and social constraints across contexts.

My research also draws on data collected in close partnership with San trackers, whose skills allowed us to reconstruct fine-scale sequences of lion hunting behavior, often days after events occurred. Their expertise goes far beyond identifying sites: by integrating traditional tracking with GPS technology, produce detailed reconstructions that capture predator and prey behaviors at a level of resolution otherwise impossible to achieve. These contributions are recognized through co-authorship and capacity-building initiatives, including formal tracker certification programs that create professional opportunities and acknowledge the scientific value of Indigenous knowledge. This integrative, community-based approach demonstrates how scientific rigor and local expertise can be mutually reinforcing. It also resonates with Deep Springs' pillars of labor, community, and service: as I work to build equitable research partnerships in Africa, I would likewise mentor Deep Springs students to see science as both intellectual inquiry and a responsibility to society, preparing them to become leaders who connect ideas with service and community engagement.

Most recently, my program has expanded to a large-scale collaring initiative. Entire prides (i.e. every individual member) are being collared across ecological gradients in Namibia, Botswana, and Zimbabwe, with devices that collect multi-modal data streams, including accelerometry, GPS, magnetometry, and audio data. With full prides already collared at all three sites and more than 40 lions expected to be collared by end-2025, this effort complements my observational and experimental work while opening opportunities to investigate social behavior at scales previously impossible. Together, these efforts define a forward-looking program that integrates technological innovation, ecological comparison, and controlled studies, while maintaining a strong foundation for student involvement and discovery.

Student Opportunities | My research program provides rich opportunities for undergraduate research. Students at Deep Springs could analyze existing datasets from my lion studies, which include high-resolution GPS, audio, and accelerometry collected across field sites spanning a gradient of resource richness. Projects might explore how ecological gradients shape cooperation, how individual variation influences movement and communication, or how tolerance of nonparticipants at kills (as in my hunting studies) can be modeled through game theory. Students could also pursue research linking animal behavior to applied conservation challenges such as human–wildlife conflict. For instance, case studies from my NGO collaborations on livestock depredation could be adapted into student-led analyses of how ecological, social, and management factors intersect, work that connects behavioral ecology directly to pressing real-world issues.

These same themes can be extended to the Deep Springs ranch, where students might investigate grazing impacts on vegetation, water use and land stewardship, or behavioral adaptation in livestock and wildlife. Such work connects ecological inquiry directly to the College's labor pillar, ensuring that academic research, community life, and service are mutually reinforcing.

Beyond independent research, these datasets also provide material for data-driven case studies and classroom activities. Students could work directly with GPS tracks, audio recordings, or accelerometry profiles to practice hypothesis testing, data visualization, and scientific writing. This integration ensures that even those not pursuing independent projects gain hands-on experience with real-world ecological data, reinforcing core skills in critical thinking, analysis, and communication.

Equally important, I would connect students to my international research network, which includes collaborators at the Max Planck Institute of Animal Behavior, CNRS in France, the University of Minnesota's Lion Center (formerly the Serengeti Lion Project), and partner NGOs across southern Africa. Through guest seminars, discussions of current research, and virtual exchanges with colleagues, students would gain exposure to leading scientists and conservation practitioners working across Africa and

Europe. These interactions broaden cultural and scientific horizons, showing students how local research links to global challenges while preparing them for lives of service and leadership in society.

Embedding Research in the Deep Springs Model | My research program is well positioned to thrive at Deep Springs. Competitive funding is already secured through 2028, ensuring continuity of field operations, collaring efforts, and data collection across field sites. I maintain guest and collaborative affiliations with institutes such as the Max Planck Institute of Animal Behavior and the University of Minnesota, which provide ongoing access to shared expertise and resources. Importantly, Deep Springs' academic calendar includes a four-month teaching release (May–August), during which I will dedicate time to conduct fieldwork, harvest data, and advance analyses. The structure of my program, which integrates large-scale collaring, observational field data, and experimental approaches, is inherently flexible, allowing me to maintain momentum in research while fully engaged in teaching and community life.

This structure allows me to remain fully research-active while also investing deeply in the close, seminar-style teaching, self-governance, and shared labor that define Deep Springs' unique environment. My prior experience living and working in remote field camps has equipped me to thrive in, and contribute to, such an isolated but intensely collaborative community. Just as I currently involve students in research and supervision, I envision Deep Springs students participating through independent projects and data-driven case studies that connect global conservation science to their own academic experience. My research interests also intersect with broader liberal arts inquiry, raising ethical, historical, and philosophical considerations about cooperation, adaptation, and the relationship between humans and the natural world, making them especially well-suited to an interdisciplinary community like Deep Springs.