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Review article

Frank Beach Award Winner: In pursuit of adventure: Studying social behavior in beautiful birds and odd rodents, as well as peering into the unknown

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ABSTRACT

How does the brain promote prosocial behavior in non-reproductive contexts and allow animals to get along in groups? I have spent 20 years pursuing answers to this question. Here I review the body of research that comprises my career to date. I use a non-traditional narrative format to detail my scientific journey, beginning with why and how I began conducting research with bees and birds as an undergraduate and graduate student, which led to exploring the brains and behavior of various rodents as a postdoctoral researcher and into my independent career as a professor. I discuss the successes and struggles I have experienced as a scientist, and how issues related to science, education, and our planet loom in my consciousness, calling into question the types of academic pursuits my future holds. Ultimately, my hope is that I provide an honest account of the wonders and hardship one can experience in the pursuit of exploring the unknown.

1. Prologue

How did I get here? I never thought I'd live in Georgia. My partner, Dr. Richmond R. Thompson (Rick) — a fellow behavioral neuroendocrinologist, and I have a lovely home in the country, complete with an Australian shepherd, fluffy cats, and chickens named after our favorite TV show characters. We're surrounded by nature. I ineffectively try to thwart voles and chipmunks from eating my tulip bulbs, squirrels from shredding our corn, and jays from stealing freshly planted seeds. We occasionally rent out our attic to small colonies of bats, let carpenter bees slowly consume the wooden balcony, keep a close eye on trees by the lake for beaver activity, and watch armadillos decorate the yard with potholes and tunnels. My commute to the city for work involves driving past a farm with a delightfully rotund miniature donkey. A primary driver for entering the field of behavioral neuroendocrinology was a love for animal behavior. I'm very fortunate to feel the presence of other species daily; we have a very good life. However, this is not where we want to live. We miss the snow and less densely populated spaces in parts of the northeast. So why are we here? What is this job that I steadfastly pursued and dedicated most of my time to for 20 years, that I've ended relationships for, left friends behind time and time again, and moved to states that I had no initial interest in moving to? We all know this about academia — we hope the right job opens up in the right place, but it does not always work out that way. So, is it worth it? What have I learned along the way and where am I going next?

2. Flying with the birds

2.1. The early days

My college experience began at community colleges in San Diego, California. I don't recall ever having heard of a PhD as a degree prior to college, and I certainly had no clue that one could conduct research for a living. As a community college student, I just assumed that a PhD enabled individuals to teach at the college level. The University of California (UC) system has a wonderful transfer program that enables community college students to acquire credits in an affordable and flexible manner that will satisfy freshman and sophomore course requirements at UC schools. After completing two years of college at Grossmont and Cuyamaca Community Colleges, I transferred to UC San Diego as a junior. I went from class sizes of twenty to hundreds and from a short walk between buildings to needing to either skateboard/bike around campus or cram into a shuttle to get to my next class on time. I was impressed with the human ability to scale behavior in groups. The

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educational format and social interactions that form the purpose and experience of school were essentially the same at a small middle school (~75 students), an average-sized high school (~1800 students), a community college (~4000 students), and a large public university (~25,000 students). Yet, I learned something entirely new at UC San Diego. In class, my professors spoke about their research. I was suddenly exposed to a whole new world — a world where one's job could be to ask questions, to wax philosophical, to design studies to seek answers to complex problems, to discover, and to explore. I had been working as a yoga instructor and a secretary at a medical clinic, so this new world intrigued me, and I was enthralled with the idea of exploring the unknown. Conducting research sounded like an adventure.

I was fortunate to have a professor who took the time to help me find research opportunities as an undergraduate. I had rough questions that piqued my curiosity — What makes human societies work effectively? How is it that my sister and I share roughly half of our genes and had the same environmental upbringing but have completely opposite personalities? Why is the brain so flexible? Why are some animals more successful than others? Are you sure I can't just be a photographer for National Geographic? Ultimately, these questions led me to office of Dr. James L. Goodson (i.e., Jim) in 2005, who was studying how sociality evolved in birds. Jim explained to me that aspects of all my interests could be addressed in research examining the neural mechanisms of social behavior. I joined his lab as an undergraduate research assistant and became involved in a project that we endearingly referred to as "Duds and Studs," which examined how the nonapeptides, vasopressin (VP) and oxytocin (OT) (Goodson et al., 2009b), as well as dopaminergic (Goodson et al., 2009a), neuronal densities and function distinguished courtship phenotypes in male zebra finches. I learned that research was a long process with a variety of different tasks that ranged from discussion and asking questions, running animals through behavioral tests, working at the bench in a wet lab, to staring at cells through a microscope. I was hooked. Conducting research was so much more variable than sitting behind a desk as a clinical secretary. As much as I loved yoga, which I still actively practice today, scientific research had an indescribable element of constant novelty that kept me engaged, excited, and motivated.

Before I followed Jim to Indiana University to pursue a PhD in Biology, I joined the lab of Dr. James C. Nieh, who was primarily studying social communication in bees. For a summer, I sat in a corn field at UC San Diego and literally painted honeybees at a sucrose feeder so that my fellow undergraduate research assistant could identify when specific individuals came back to the hive and exhibited distinct signals and waggle dances, directing other bees in the colony to a food source. It was then my job to puff alarm pheromones (i.e., a crushed-up bee in a needleless syringe) over a sucrose-feeding bee, who would carry information about danger back to the hive, eventually leaving me alone at a sucrose feeder in a corn field, no bees in site. However, I wasn't really alone — this was San Diego, after all, and the corn field, which was primarily used by plant geneticists, was adjacent to a massive freeway system littered with people in cars. I had a lot of time to myself in that corn field, and the younger version of me interpreted the mess of freeway driving and traffic patterns as an impressive display of human cooperation. I now view many commonplace human behaviors as tolerance rather than cooperation, but at the time I was inspired by people, birds, and bees to study how the brain modulates social behaviors that enable some species to successfully live in large groups.

2.2. 1000 surgeries

Jim Goodson had established a beautiful comparative model for examining how closely related estrildid finch species evolved a gregarious phenotype. In the lab at Indiana University, we had five species of estrildid finches that were all socially monogamous but varied in group size: violet eared waxbills (territorial), melba finches (territorial), Angolan blue waxbills (moderately social), spice finches (highly social), and zebra finches (highly social). Although Jim examined the involvement of several neuropeptides in social behavior, the lab focused heavily on the role of nonapeptides in gregariousness. The VP/OT nonapeptides had been identified as key modulators of a variety of social behaviors, including aggression, pair bonding, and parental care (Neumann et al., 2001; Young and Wang, 2004; Albers et al., 2006). Additionally, Dr. Larry J. Young had found that OT/VP receptor densities and distributions distinguished mating systems in voles (Young, 1999). Through immediate early gene studies, Jim found that VP neurons in the bed nucleus of the stria terminalis (BNST) were responsive to exposure to a same-sex conspecific in gregarious finches, but not territorial finches; further, gregarious estrildids had greater BNST VP neuronal densities compared to their territorial relatives, suggesting that BNST VP neurons promote nonreproductive social behavior (Goodson and Wang, 2006). These findings, among others, set the stage for my dissertation research while a graduate student at Indiana University. Although the Goodson Lab was accumulating papers showing an involvement of VP/OT in social behavior, most of these studies were correlative in nature and causal studies were needed to demonstrate the direct contributions of nonapeptide neurons to behavior. You know that saying — "Luck is preparation meeting opportunity?" I wholeheartedly believe in that adage. My timing as a graduate student in the Goodson Lab couldn't have been better. The groundwork of correlative studies had been laid, and the technology was developed and just required validation. In collaboration with his best friend from grad school, Rick Thompson (yes, that's my partner now; he's my life partner and my academic uncle… just let that simmer for a while), Jim had generated antisense oligonucleotides to block translation of mRNA into peptide, which would allow for site-specific knock down of VP (or OT) production. All that was needed was a workaholic young scientist with dexterous hands, patience, and an eagerness to understand how distinct components of the brain (i.e., cell types and regions) modulate specific types of social behavior. I was that workaholic young scientist, and I found doing neurosurgeries on birds to be quite fun, which was a good thing because I ended up doing just over 1000 surgeries during my six years as a graduate student.

In 2008, most research about the nonapeptide system examined VP and OT receptors, and fewer studies assessed nonapeptide-producing neurons. Just as VP and OT receptors are distributed throughout the brain (Insel and Shapiro, 1992; Insel et al., 1994), VP- and OT-peptide producing neurons are located in distinct cell populations, with differential projections targeting a variety of brain regions (Rood and De Vries, 2011; DiBenedictis et al., 2017). The field knew a fair amount about behavioral functions of nonapeptide receptors in specific brain regions; for example, studies had shown that VP receptor activation in the ventral pallidum was necessary for pair bond formation in male prairie voles (Lim and Young, 2004), OT receptors in the nucleus accumbens regulate partner preference in female prairie voles (Ross et al., 2009), VP receptors in the lateral septum promote social recognition in rats (Everts and Koolhaas, 1999), and VP receptors in the septum facilitate aggression in male zebra finches (Goodson and Adkins-Regan, 1999). However, we knew little about where the peptide was coming from that act on those receptors to modulate behavior. Does VP produced in the BNST primarily serve different behavioral functions than VP produced in the paraventricular nucleus of the hypothalamus (PVN), for example? For my dissertation research, I used antisense oligonucleotides to knock down specific VP and OT (as well as vasoactive intestinal polypeptide) cell groups in zebra finches, Angolan blue waxbills, and violet-eared waxbills to determine the direct contributions of distinct VP/OT cell groups to social behavior. The ultimate goal was to add to the existing literature and ongoing research on nonapeptide-mediated social behavior and provide a more comprehensive understanding of how VP/OT modulate behavior by examining social contexts beyond reproduction (i.e., pair bonding and parental care).

My first study targeted the VP neuronal population of the BNST in male zebra finches (Fig. 1) and found that antisense knockdown of this cell group decreased the inherent zebra finch preference to affiliate with

Fig. 1. For some reason I never photographed the zebra finches. However, when dabbling with watercolor, I did paint them. Clearly, painting bird feet was not my forte.

a large over a small group of same-sex conspecifics (Kelly et al., 2011). A follow-up study then examined the functional significance of male-biased production of VP within the BNST; males of most species have more BNST VP neurons than females. This study showed that BNST VP knockdown had no effect on group size preference or aggression in female zebra finches but enhanced aggression and impaired courtship in males (Kelly and Goodson, 2013b). Together, these findings not only demonstrated the first causal evidence of BNST VP function, but they also suggested that the ancestral function of BNST VP in male zebra finches may have been to facilitate intraspecific territoriality in competitive reproductive contexts, as well as courtship, but that this cell group was later co-opted to also modulate non-reproductive flocking preferences in males. Further evidence to support the idea that BNST VP may have evolved for purposes other than group size preference came from a study in the moderately social Angolan blue waxbill (these really lovely birds are less gregarious than zebra finches); we found that BNST VP knockdown did not influence group size preference in males or females but did generally decrease affiliative contact in both sexes (Kelly and Goodson, 2013a). Importantly, the studies in male and female zebra finches and Angolan blue waxbills demonstrated that while BNST VP modulates social behavior in closely related species, there are notable species-specific effects on behavior. So, although there is some evolutionary conservation in nonapeptide function, the system is plastic enough to also allow for variation in behavioral modulation over time. At this juncture, I became curious about whether VP was involved in modulating female zebra finch group size preferences. Even though manipulation of the BNST VP cell group did not influence such a preference in females, the female birds still exhibited a robust preference to affiliate with large groups, so something in the brain had to be responsible for that preference (Fig. 2)!

We generated antisense oligos to target OT neurons, and I next targeted the PVN OT and VP cell groups — the largest sources of nonapeptides in the brain (Moore and Lowry, 1998). More surgeries. More knocking down of peptides. We found that PVN VP facilitated a preference for a large group in both male and female zebra finches, whereas PVN OT promoted this preference only in females (Kelly and Goodson, 2014a). This project was time intensive and used a lot of birds, so we decided we wanted to get as much information out of these subjects as possible. Therefore, in addition to examining non-reproductive social behavior, I also tested subjects in a reproductive context. I have fond memories of conducting "colony tests," which entailed placing a mixed-sex group of 9 novel zebra finches into a large cage and watching them sort out group dynamics over the course of a few days. I would sit behind a blind (i.e., lab bench paper) and peer through a cutout like a creeper. With my iPod playing the soundtrack to Downtown Abbey in my ears, I sat behind that blind for hours, day after day, speaking into a recorder, detailing the movements of one bird at a time. To this day, if I see a scuffle at a bird feeder, I hear myself note "beak fence" or

Fig. 2. Molecular biology bootcamp 2013. From left to right: Dr. Marcy A. Kingsbury, Dr. James L. Goodson, and Dr. Aubrey M. Kelly. Marcy had a legitimate understanding of molecular biology. Jim and I tried, but we really left that bootcamp with a legitimate appreciation for the croissants made by Tart Baking Co. in Northampton, Massachusetts.

"displacement!" The Downton Abbey soundtrack likely amplified this effect, but watching finches in colony tests really made me appreciate studying an organism with primary modes of communication – vision and audition – that are similar to our own. Bird social interactions generate dramatic content that would be great material for a soap opera. I would also soon learn that studying rodents, which primarily communicate via olfaction, would be a different, less exhilarating ball game. Fond memories aside, this last experiment exploring nonapeptide neuronal function demonstrated that the PVN OT cell group was critical for typical exhibition of pair bonding behaviors in both male and female zebra finches, with stronger effects in females (Kelly and Goodson, 2014a). These findings reflected those of previous studies that showed that activation of OT receptors is necessary for pair bonding in female but not male zebra finches (Kabelik et al., 2009; Pedersen and Tomaszycki, 2012; Klatt and Goodson, 2013) and for female but not male prairie voles (Young et al., 2011), suggesting evolutionary conservation of sex-specific effects on OT-mediated behavior.

What did we learn from those ~1000 surgeries? The bulk of my graduate studies was synthesized in a review that detailed what we know about contributions of distinct VP and OT cell groups to behavior (Kelly and Goodson, 2014b). In collaboration with Jim and other members of the Goodson Lab, we expanded our knowledge about nonapeptide-mediated behavior by focusing heavily on non-reproductive social contexts, and we demonstrated both evolutionary conservation and plasticity in neural mechanisms underlying sociality by studying a variety of species. I also learned on an unexpected hallucinogenic trip (turns out there were ingredients in that chocolate bar that I was unaware of) in 2015 that there are heavy costs associated with the pursuit of knowledge; laying semi-catatonic in a garden, I felt a substantial weight as I watched countless birds fly by in a prolonged hallucination. What the world could see was a productive graduate career that generated new insights about neurochemical mechanisms that shaped the evolution of complex social behaviors and multiple products in the form of 13 publications. However, what they could not see were the studies that went nowhere and a great many birds that

stopped flying. What we do can sometimes feel quite heavy.

2.3. Looking for change

As a graduate student, I observed a striking amount of evolutionary conservation of VP/OT anatomy and function and was curious about the extent of neuro-anatomical/functional conservation across taxa. Does the BNST VP cell group also promote grouping and affiliative preferences in highly social mammals or did other mechanisms arise to promote social preferences in mammals? I also grew slightly envious of all the neuroscientific tools that were available for rodent, but not bird, research. Lastly, Jim had warned me about the difficulties of obtaining NIH funding for avian research, so expanding my scientific toolkit to incorporate the ability to work with taxa other than birds seemed like a wise idea. I decided to seek a postdoctoral research position that would allow me to continue examining how the brain modulates social behavior but to expand my horizons by conducting such research in a rodent. I had read dozens of papers about "the highly social" prairie vole and had identified the lab of Dr. Alexander G. Ophir (i.e., Alex) as the perfect fit for the next step in my academic career.

3. An interlude with voles

3.1. Lessons on the importance of language

Upon receipt of a National Institutes of Health (NIH) NRSA F32 grant, I joined Alex's lab at Cornell University in August 2014. Two weeks after I moved from Bloomington, Indiana to Ithaca, New York, Jim passed away after a long battle with cancer. I lost an immensely valued friend and mentor. Had I not met and worked with Jim, I wouldn't have pursued a PhD or be an academic today. Jim had attended graduate school and conducted a postdoc at Cornell, and he was so excited for me to move to his old stomping grounds. Before he passed away, he had made a long list of forests and hiking trails to visit and introduced me to his "academic parents" Dr. Elizabeth Adkins-Regan and Dr. Andrew H. Bass (and Midge Marchaterre!). It felt like I had family in Ithaca, which made the transition of moving to a new place, starting a new position, and losing a dear friend all at once more seamless than it otherwise could have been. Plus, Jim was buried at a natural cemetery preserve just a few miles from the house I was renting outside of Ithaca, so I was able to visit his memory often. The preserve was a great place for a Deadhead (a Grateful Dead fan) hippie to be put to rest. There were no headstones, and Jim's burial site was quickly overgrown with plants. I spent many early mornings birding and many late nights photographing stars and fireflies in those fields.

Alas, I was not in upstate New York to enjoy the scenery and wildlife (Fig. 3). I threw myself into work and Alex trained me how to conduct behavioral tests with prairie voles. Within the first few days of working with prairie voles, I quickly realized that "the highly social prairie vole" has some serious limitations for when they are highly social! I was accustomed to zebra finches that live in flocks of hundreds and, although they can certainly be aggressive, are overwhelmingly gregarious in a variety of contexts. Zebra finches often exhibit prosocial behavior with same-sex conspecifics at every age, but I learned that prairie voles are much more likely to be antisocial and even aggressive if two adult, same-sex strangers interact. Prairie voles are indeed "highly social," but primarily only with their pair bond partner, offspring, and familiar siblings. Prior to joining Alex's lab, I had largely paid attention to prairie vole neuroscience research and had not read the extensive literature detailing field work in voles. I realized I had a lot to learn about behavioral ecology. Other than learning how to use power tools (thanks, Alex!), the most valuable thing I learned as a postdoc was how to consider an organism's behavioral ecology when generating scientific questions and designing experiments. In 2015, Alex and I published an opinion piece that not only promoted the use of comparative approaches to understand the evolution of the brain and behavior but also stressed the importance of considering a species' behavioral ecology and carefully defining how we use umbrella terms such as 'social' (Kelly and Ophir, 2015).

Prairie voles do not exhibit a preference to affiliate with a large group like zebra finches because they did not evolve to live in large groups! Therefore, I was unable to ask the question "does BNST VP modulate grouping preferences similarly in finches and voles." However, I was able test whether BNST VP exhibited *some* functional conservation across taxa. The Ophir Lab had previously noticed that prairie voles were more likely to be affiliative in non-reproductive contexts prior to sexual maturity. Intuitively, this made sense; young animals are more vulnerable than adults and often depend on communal members for survival (Shapiro and Insel, 1990; Curley et al., 2009). However, the physiological needs of an organism shift as they develop, and thus behavior is likely to shift as an animal transitions into different life history stages (i.e., from offspring in a family to an adult that must establish an independent territory and compete for a mate). To examine the developmental trajectory of non-reproductive affiliation in prairie voles, I conducted an immediate early gene study to quantify VP neural responses associated with interactions with a same-sex novel peer in male prairie voles at four different ages: postnatal day (PND) 15 (i.e., pre-weaning), PND 30 (early adolescence), PND 45 (rough onset of sexual maturity), and PND60 (adulthood). We found that affiliative

Fig. 3. Treman Falls throughout the seasons. Ithaca, New York.
Photography by Aubrey Kelly.

behavior decreased and antisocial (i.e., nonsocial and aggressive) behavior with novel peers increased post-weaning. Similarly, BNST VP neurons were more responsive to interacting with a same-sex novel peer at pre-weaning, corresponding to when a male vole is most affiliative in a non-reproductive context. Further, regardless of age, BNST VP neural responses positively correlated with prosocial contact and negatively correlated with aggression (Kelly et al., 2018). This reflects previous findings in the finches (Goodson and Wang, 2006; Kelly et al., 2011; Kelly and Goodson, 2013a), suggesting that there are conserved affiliative functions of this cell group across taxa — at least in several finch species and in prairie voles.

3.2. A love-hate relationship with development

Other than wanting to gain experience working with rodents, a major goal of my postdoc was to incorporate a developmental approach into my research. I was interested in developmental plasticity of the nonapeptide system. What factors influence VP/OT anatomy and function? How does an animal's early experiences with parents and family dynamics influence their neural and behavioral phenotype as an adult?

The aims in my NRSA grant entailed examining how variation in parental care influenced development. With Alex's expertise in behavioral ecology, we designed a study that manipulated the amount and quality of parental care prairie vole pups received. We used an ecologically relevant design so that we would be more likely to observe behaviors that reflect those that occur in wild populations. For instance, in the wild, vole parents must forage for food, whereas in the lab, vole parents are housed in standard rodent cages and have access to low risk, high energy food ad libitum, which presumably alleviates energetic demands and natural trade-offs that parents experience in nature. Importantly, field studies show that prairie vole offspring naturally experience different types and amounts of parental care. Thus, to loosely mirror a real-world tradeoff that parents experience, I raised prairie vole pups i) in the presence or absence of a father, and ii) with parents that experienced a tradeoff in caring for their offspring or caring for themselves. To force this tradeoff, we created home cage environments that required parents to leave the nest to obtain food — something that occurs in wild populations. Food was placed in a wire hopper at the end of an ~5 ft plexiglass tube attached to the home cage. For parents in the Tradeoff condition, the plexiglass tube was set at a 20° incline. Notably, suckling prairie vole pups latch to mothers' nipples with milk teeth, and they hang on for dear life, so to speak. The incline of the tubes was steep and slippery enough such that mothers could not successfully climb to the top of the tube where the food hopper was with suckling offspring in tow; in order for mothers to obtain food, they had to forcibly detach their pups and leave them behind at the nest. This design imposed a moderate energetic cost on parents; to feed, they were forced to climb a modestly steep incline at a distance not encountered under normal laboratory housing. Parents that did not undergo the tradeoff manipulation lived in cages with a plexiglass tube that was at the same level as the home cage (i.e., no incline), allowing mothers with suckling pups to take offspring with them to feed and for parents to exert nearly normal levels of effort to obtain food. Perhaps one of my favorite findings from this project was that single mothers compensated for the lack of a coparent and they brooded their pups more than mothers of biparental families. When mothers were faced with a tradeoff, they chose to invest in their pups (i.e., they ate significantly less than biparental mothers). However, when fathers were faced with a tradeoff, they chose to invest in themselves. This design significantly affected parental behavior and the quantity and quality of parental care that pups received. Interestingly, the complete absence of a father influenced pup social behavior less than low quality paternal care experienced in the Tradeoff condition (Kelly et al., 2020).

With the assistance of Dr. James P. Curley and Dr. Frances A. Champagne, I was able to include an epigenetic component to my project. Therefore, in addition to examining behavioral outcomes in pups raised with variable parental care, we also assessed OT receptor (OTR) and VP 1a receptor (V1aR) gene expression and DNA methylation status of the V1aR gene (*avpr1a*). Ultimately, we found that male prairie voles raised in the Tradeoff condition (i.e., received less paternal care) exhibited impaired social approach behavior and increased V1aR gene expression in the lateral septum, which in turn related to DNA methylation of the *avpr1a* gene in the lateral septum (Fig. 4). Because of a careful consideration of real-world behavior, we produced a neurobehavioral dataset that generated insight into how family context and co-parent interactions alter caregiving and impact epigenetic modifications in the brain and adult behavior of offspring (Kelly et al., *Science Advances* 2020).

So, why do I have a love-hate relationship with development? As an undergraduate I was fascinated by how the early life environment can drastically alter the life trajectory of an animal. Today, I still love thinking about developmental questions and research. However, as anyone who studies development knows, developmental research is incredibly time consuming. It took 4 years simply to collect the data for this single project and 6 years from the time the project started to the time of manuscript acceptance for publication. Unfortunately, the academic clock is not necessarily forgiving of time-consuming research. It was nerve-racking to be on the academic job market without yet having my biggest postdoc project publicly available for search committees to see; this is a feeling I know several postdocs experience. Furthermore, we have little to no control when a rodent will give birth to pups. Therefore, developmental projects typically require that an experimenter be in the lab every day — on weekends and over holidays, I needed to check whether my subjects were born and ready for early life manipulation. This wasn't too dissimilar from my graduate work given that the antisense oligos required an injection schedule of every 12 h; for most of my graduate career I either worked long days or returned to the lab at night. In the early days I didn't mind spending most of my life in the lab. However, over time, my desire for a personal life and better boundaries with work began to grow.

4. Succeeding and struggling with spiny mice

4.1. A fortuitous job interview

Although there are several rodent species available for the study of reproductive social behaviors, there are surprisingly few that are ideal for studying non-reproductive social behaviors. As a postdoc, I learned that while prairie voles are an excellent organism for studying pair bonding, parental care, and family dynamics, they are neophobic and quite aggressive with strangers. Furthermore, prairie voles live in small family groups and do not naturally live in large groups of related and

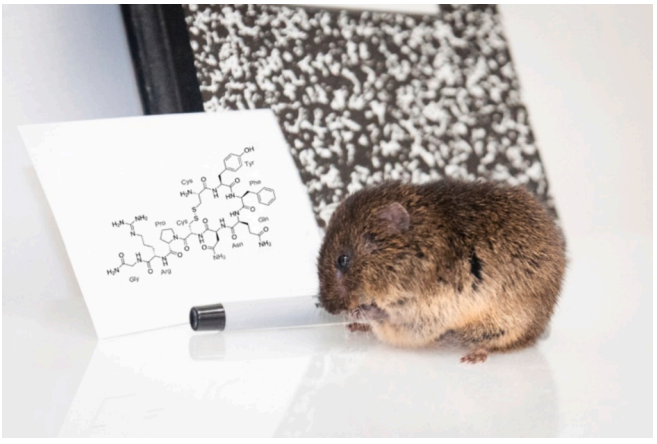

Fig. 4. A studious prairie vole, hard at work.
Photography by Aubrey Kelly.

unrelated individuals. Yet my desire to study grouping behaviors in mammals persisted, so I began searching for a lab-tractable rodent that was highly social and lives in large groups in the wild. When I was on the job market for a position as an Assistant Professor, I was proposing to establish a lab that studied social behavior using prairie voles. I have a bit of a problem with being overly honest, and at the end of my job talk I lamented how prairie voles weren't the highly social rodent of my dreams and that I yearned to find a rodent that exhibited similarities to the lovely little zebra finches that I had once worked with; I wanted to find a rodent that I could bring into the lab that would/could be highly social in nearly every social context. This was how I met my now collaborator Dr. Ashley W. Seifert at the University of Kentucky. Ashley is a regenerative biologist who studies the remarkable ability of African spiny mice to regenerate entire suites of tissue (Seifert et al., 2012). On my job interview, he showed me his animal colony, which consists of dozens of large cages containing same-sex, mixed-genetic relation groups of 20–30 spiny mice each. He plucked one adult mouse out of a cage and added it to another cage, and I watched in awe as the little mouse casually joined his new group. If one were to do that with an adult prairie vole, lab mouse, or rat, particularly with males, chaos would have erupted in the cage, likely ending with a dead animal if there were no intervention from an experimenter. I have since learned that spiny mice too have their limits and can exhibit aggressive behavior, but they are by far the most prosocial, least aggressive rodent I have ever worked with or observed. Fortunately for me, Ashley appreciated my ideas for using spiny mice to study grouping behavior and later graciously helped me set up a breeding colony of spiny mice in my own lab at Emory (Fig. 5). A fortuitous job interview indeed.

I had a second fortuitous job interview — the job interview that led to my job as an Assistant Professor at Emory. I never had any intention of moving to Georgia prior to going on the job market, and in full transparency, of all the places that I had lined up for job interviews, Emory was initially at the bottom of that list. I had no desire to move to the south simply because I'm in love with cold, snowy, desolate places. However, when I visited, Emory felt, professionally, like the right institution for me. I vividly recall standing at a reception on my interview and thinking, "****, I'm moving to Georgia." It is not my intention to be harsh toward Georgia or the south. Georgia is a fine place to live and is ideal for many people! It is just not *my* preference. Indeed, many people I know really dislike living in the north because it is so cold for so long; while the north isn't the ideal place for them, it just happens to be my happy place. However, for years I had been prioritizing an academic career over where I would ideally like to live, and the option to *not* move to Atlanta, Georgia never seriously crossed my mind. I was excited to launch my independent career as a scientist. I'll note that this excitement was dampened by the fact that my partner, Rick, and I had to figure out how he could move from Bowdoin College in Maine to join me in Atlanta. Academia is typically not very forgiving of relationships. We were extremely fortunate, though, and Rick was given a position as a professor at Emory Oxford College, located about an hour outside of Atlanta. We were lucky that we were able to obtain two academic jobs roughly in the same city, but I was more fortunate that I met a man who was willing to follow me for my career. So, we moved to Georgia. You rarely really get a choice in where you live as an academic. You're lucky enough just to get a job, no matter how qualified you may be. It saddens me today to hear graduate students dream about where they'd ideally like to get a job as a professor (I too once dreamed of living in Oregon, Vermont, Maine, Colorado, Minnesota, or Massachusetts), and it breaks my heart to see postdocs putting off starting their lives (i.e., settling down) as they wait and hope for an opportunity that simply won't materialize for everyone. I was one of the lucky ones — I got a job, and I stumbled upon the perfect little rodent for my research aspirations.

Fig. 5. A huddle puddle of spiny mice, all novel to one another. Photography by Aubrey Kelly.

4.2. *Laying a foundation*

In the wild, spiny mice (*Acomys dimidiatus*) are found throughout Africa, the Middle East, and Southeastern Asia (Nowak, 1999; Deacon, 2009; Frynta et al., 2011). Historically, spiny mice were used for studying obesity because they have a tendency to overeat and develop Type 2 diabetes in the lab (Gonet et al., 1966; Shafrir, 2000). Today they are predominantly used for regenerative research, and quite impressively are the only mammal documented to date that can completely regenerate damaged tissue (Maden and Varholick, 2020; Seifert and Temple-Smith, 2022). In the last decade, spiny mice have also been used as a model for studying human-like reproductive biology because, unlike most rodents, they exhibit a menstrual cycle (Bellofiore et al., 2017; Bellofiore et al., 2018). A few studies from the early 1980s had revealed that spiny mice are communal breeders and are highly social, living in large groups comprised of related and unrelated animals (Porter et al., 1980; Porter et al., 1983; Porter, 1988). These studies and observations of spiny mice in the wild strongly suggested this species would be an excellent candidate for studying sociality in non-reproductive contexts. However, social behaviors had yet to be systematically characterized for spiny mice, and there was also a lack of basic anatomical knowledge of social neural circuitry. In 2019, I was awarded a Klingenstein-Simons Fellowship in Neuroscience to lay a behavioral and neural foundation for conducting social neuroscience experiments in spiny mice. The first studies with spiny mice conducted in my lab at Emory therefore aimed to characterize basic social behaviors and preferences and to map VP/OT circuitry. I characterized distributions of VP and OT neurons, revealing widespread sex differences in OT neuronal populations (Kelly and Seifert, 2021). In collaboration with Dr. Larry J. Young's lab, we conducted receptor autoradiography and RNAscope to also map distributions and quantify sex differences in VP/OT receptor protein and mRNA (Powell et al., 2022). Lastly, we conducted a systematic characterization of social behaviors in spiny mice and demonstrated via several paradigms that this species is indeed highly prosocial in reproductive *and* non-reproductive contexts, exhibits very little aggression, and is highly gregarious (i.e., prefers to affiliate with large over small groups) (Fricker et al., 2021). Thus, spiny mice are ideal for studying social behavior, particularly prosociality, in both males and females in non-reproductive contexts.

Because we are interested in understanding the neural mechanisms underlying social behavior in spiny mice, we also spent years validating technology to manipulate and record from the brain. Seven years on, and we now have the ability to manipulate specific brain regions, distinct cell types, and neural circuits, as well as to obtain real-time neural recordings of calcium signaling via wireless fiber photometry. This was all made possible because of my exceptionally talented first graduate student Dr. Brandon A. Fricker and the help of colleagues and friends, including Dr. Zoe R. Donaldson, Dr. Malavika Murugan, Dr. Larry J. Young, and Dr. Arjen J. Boender, as well as support from

mentors and friends, including Dr. Hans A. Hofmann and Dr. Donna L. Maney.

There are pros and cons to most things in life. Introducing a new species to the field of social neuroscience meant that we could do virtually anything that entailed social behavior and the brain and be the first people to do it in this species; there were and still are ample opportunities for making novel contributions to the fields of animal behavior and neuroscience. The downside was that we had to start *everything* from scratch. We couldn't start conducting hypothesis-driven experiments until we knew what we were working with. I don't know that I would recommend this approach as a new faculty member starting a lab! Starting a new research program with a species new to the field was one hell of a gamble so early on in my independent career. However, some of my predecessors succeeded at this in the past (i.e., those that first worked with prairie voles), and it was a gamble I was willing to take. I intentionally maintained prairie vole research for a few years so that I would have a cushion to land on if the spiny mouse research program failed to launch. For three years, I had three species, and therefore three breeding colonies, in the lab — spiny mice, prairie voles, and Mongolian gerbils. When at conferences or seminars, I had numerous graduate students and postdocs express how I was "living their dream" of being able to work with so many species at one time, and I was told more than a few times that trainees hoped to run a research program similar to mine someday. However, it was never my intention to have a menagerie of animals in my lab, and I strongly recommend against starting a lab with multiple species, except for established comparative models such as prairie and meadow voles. Maintaining colonies of multiple species is expensive and a lot to juggle while also conducting research, writing grants, teaching, mentoring trainees, managing a lab, and doing all the service that's required of faculty. I had multiple species in my lab primarily because I was stubborn and wanted my "zebra finch of the rodent world." However, I was fully aware that I was taking a risk with the spiny mice, so I wanted my bold venture to be backed by a prairie vole research program that was tested, tried, and true. In the end, things have worked out with the spiny mice — for now, at least.

4.3. The failed comparison

I have always admired studies that compare closely related species to determine how unique selective pressures have "pushed" the brain and behavior in distinct directions. Although there are multiple *Acomys* species (potentially up to 26 (Aghová et al., 2019)), *Acomys dimidiatus*, formerly referred to as *Acomys cahirinus*, is the primary spiny mouse species being studied in laboratory settings. Field studies have indicated that spiny mice of the genus *Acomys* live in Middle Eastern deserts in mixed-sex groups ranging from 12 to 46, with multiple *Acomys* species coexisting on the same territory (Shargal et al., 2000). Additionally, field studies in food-abundant habitats near more urban centers have documented *Acomys* groups in much higher densities (Shkolnik and Borut, 1969). While we know spiny mice, specifically including *Acomys dimidiatus*, live in large groups in the wild, we still lack behavioral ecology data from field studies like that of the prairie vole community. Further, we also lack the ability to readily obtain other *Acomys* species for comparative studies. Because we do not know whether there is an *Acomys* species that is less social than *Acomys dimidiatus* and because we do not have access to other *Acomys* species, I sought alternative organisms for comparison. Although the name is deceiving, spiny mice are actually more closely related to gerbils (Gerbillinae) than they are to true mice (Murinae) (Chevret et al., 1993; Fabre et al., 2012; Steppan and Schenk, 2017). Conveniently, one can order Mongolian gerbils (*Meriones unguiculatus*) from commercial businesses. Mongolian gerbils have a behavioral ecology that is extremely similar to prairie voles; they are socially monogamous, biparental, and live in small family groups. Having now personally conducted many behavioral tests with both prairie voles and Mongolian gerbils, I can also say that the gerbils, while somewhat territorial, are more affiliative with same-sex strangers than prairie voles. Ultimately, Mongolian gerbils were the best option available to use as a less social comparison to spiny mice, and therefore I decided to attempt to use spiny mice and gerbils as a comparative model (Fig. 6).

We conducted a comparative study that demonstrated that, as one would expect, spiny mice are substantially more gregarious than gerbils when tested in a group size preference test. Additionally, in a non-reproductive social interaction with a novel, same-sex conspecific, male and female spiny mice are more prosocial than male and female gerbils; further, spiny mice exhibit little to no aggression, whereas the majority of gerbils exhibit some aggression in a non-reproductive social interaction (Gonzalez Abreu et al., 2022). I submitted a grant proposal to the National Science Foundation for which the long-term goal was to identify brain mechanisms that support diversity in prosocial behaviors and identify evolutionary adaptations that gave rise to variation in their expression. I proposed to do this by departing from investigations of the commonly studied prosocial behaviors that occur in reproductive contexts and instead examining the neural mechanisms underlying non-reproductive prosocial behaviors. Using a comparative approach, this proposed research would elucidate neural mechanisms associated with different levels of non-reproductive sociality in two rodents, the gregarious, highly social spiny mouse and the moderately social Mongolian gerbil. Aside from our one comparative study published in iScience (Gonzalez Abreu et al., 2022), this particular comparative approach would not bear more fruit. The NSF grant panel was not compelled by the degree of relatedness between spiny mice and gerbils, which was a perfectly fair criticism. It was clear that there was no future in which I would be funded for comparative research using both spiny mice and gerbils. And where there is no money, there is no research. Adapt and keep going. Through working with the gerbils, I at least discovered that they were excellent for another line of research — examining mechanisms that rapidly allow an animal to switch from prosocial to aggressive behavior. This resulted in a fun collaboration with my partner, Rick, who has studied steroid-mediated behavior for much of his career, in which we somewhat surprisingly learned that testosterone can facilitate prosocial interactions in both males and females in specific social contexts (Kelly et al., 2022; Kelly and Thompson, 2023).

4.4. Brain regions, cell types, and circuits that facilitate mammalian non-reproductive sociality

We have had, at least what I consider to be, several successes with determining how the brain facilitates mammalian non-reproductive

Fig. 6. Like the prairie voles, Mongolian gerbils were also quite studious. Photography by Aubrey Kelly.

prosocial behavior. Through immediate early gene and neural tracing studies, we found that PVN OT may gate social reward in non-reproductive contexts via influences on reward circuitry (e.g., tyrosine hydroxylase neurons in the ventral tegmental area) in spiny mice (Gonzalez Abreu et al., 2022). Complementing this study, we also recently found that OT receptors in reward-related regions facilitate non-reproductive prosocial behavior in spiny mice as they do reproductive prosocial behavior in prairie voles (Keebaugh and Young, 2011; Keebaugh et al., 2015). Using a custom CRISPR virus designed and generated by Dr. Arjen J. Boender and Dr. Larry J. Young (Boender et al., 2023), we site-specifically knocked down production of OT receptors in the nucleus accumbens of male spiny mice. Knockdown animals exhibited significantly less huddling with same-sex strangers and consumed fewer giant mealworms (yes, they were giant) compared to control animals (Fricker et al., 2025). These findings suggest that accumbal OT receptors do not specifically modulate social behaviors but may more generally modulate reward. Further, because accumbal OT receptors facilitate partner preference formation and maternal care in prairie voles (Young et al., 2001; Olazabal and Young, 2006; Keebaugh et al., 2015), maternal care in transgenic mice (Witchey et al., 2024), and huddling with strangers in spiny mice (Fricker et al., 2025), there appears to be strong evolutionary conservation of accumbal OT receptor social function, such that these receptors facilitate prosocial behavior across rodent species that vary in breeding system and group structure.

At this juncture, we had a fair amount of data demonstrating that spiny mice will behave prosocially with conspecifics of any type (i.e., novel, familiar, kin, non-kin, same-sex, opposite sex), but we were curious if they would exhibit any biases in a group comprised of multiple conspecific types in a non-reproductive context. In a group interaction test containing novel and familiar kin and non-kin, we found that spiny mice are preferentially more prosocial with novel kin, and affiliate more with novel kin even over familiar kin. This suggested that upon formation of a new group, developing strong ties with novel kin individuals may be particularly advantageous. To identify brain regions and cell types involved in processing conspecific type, we conducted immediate early gene studies, revealing that the lateral septum differentially processes kin from non-kin (Fricker et al., 2023), whereas BNST OT neurons differentially respond to novel vs. familiar conspecifics (Esquilin-Rodriguez et al., 2025).

The lateral septum, which was identified as a susceptible brain region to variation in parental care in prairie voles from my postdoc research, continued to be a hot spot for social behavior. To identify neural circuitry that facilitates the basic drive for a highly social species to affiliate with large groups, we conducted an immediate early gene study that demonstrated that the lateral septum is more responsive to exposure to a large than a small group. Next, to determine regions that send information to and receive information from the lateral septum, we injected retro- and antero-grade viral tracers into the lateral septum of spiny mice and conducted another immediate early gene study to identify up- and down-stream targets of the lateral septum that differentially respond to large vs. small group exposure. An upstream region of interest was the anterior cingulate cortex (ACC) — a region crucial for attention, social communication, and consolation behavior (Bush et al., 1999; Burkett et al., 2016; Rose et al., 2021). We hypothesized that the ACC specifically sends social group size information to the lateral septum to at least attend to and potentially promote the preference for affiliating with a large group. Using Cre-dependent designer receptors exclusively activated by designer drugs (DREADDs), we found that inhibition of the ACC-lateral septum circuit impaired investigative preferences in male and female spiny mice, and that this circuit is necessary for male spiny mice to prefer affiliating with a large group. In fact, inhibition of this circuit actually reversed male affiliative preferences, yet did not influence female affiliative preferences. Further, this circuit specifically modulates *social* group size preferences given that inhibition did not influence behavior in a group size preference test with rubber ducks (Fricker et al., 2024). We have been thus far left perplexed as to what circuitry facilitates the basic drive for female spiny mice to affiliate with large groups. From the immediate early gene and neural tracing study just discussed, we also identified that the lateral hypothalamus, a region that receives projections from the lateral septum, was more responsive to large group exposure only in females. Studies in mice have demonstrated that the lateral hypothalamus is important for learning social rank (Padilla-Coreano et al., 2022). So, perhaps this brain region is involved in modulating grouping preferences in female spiny mice?

In a follow-up study, we used DREADDs to inhibit the lateral hypothalamus of females. Alas, we found no influence of manipulation on group size preference, affiliative or investigative. For now, neural circuitry facilitating affiliative preferences in female spiny mice remains a mystery. However, we did learn something new and valuable from this experiment. We had also conducted group interaction tests in which our female subjects interacted with a novel, previously established group of same-sex conspecifics. Control females readily interacted with and investigated members of the group, however, after an initial bout of investigation, they maintained distance from the group throughout an hour test. Yet, the experimental females that had their lateral hypothalamus inhibited immediately behaved as if they had always belonged with the novel group; they were less avoidant and more prosocial. While only one of 22 control subjects huddled with the group, all but a single experimental female huddled with the novel group (Roshko et al., In Prep). Although the lateral hypothalamus does not influence group size preference in female spiny mice, it clearly regulates decisions to approach and affiliate with novel peers. Conclusive results aside, there was something about this study that struck me as particularly interesting — as long as the newcomer was bold enough to attempt joining the previously established group, she was able to join the group. There was no resistance from the group (we observed zero aggression in every group interaction test), and rather, any hesitation for affiliating with the group fell on the shoulders of the newcomer. Anxiety — it plagues all creatures, great and small, I suppose. This study highlighted the extremely tolerant nature of [at least] female spiny mice, and tapped into something that has been nagging me for years — are highly social animals really just highly tolerant? Time will tell if I can someday disentangle social tolerance from a solid desire to affiliate in a group.

Our ongoing and future studies are now not only examining prosocial behavior in non-reproductive, but also reproductive and more ecologically-relevant, contexts. Although spiny mice evolved to live in large groups and our colleagues at the University of Kentucky are able to house spiny mice in groups of up to 30 (Haughton et al., 2016), it has taken many years to gain approval at Emory to house spiny mice in groups larger than 5. We have finally achieved this small, but nontrivial, goal, and are rather excitingly in the process of scaling everything up — from bigger test chambers to bigger groups. My hope is that we can, in our own small way, continue to contribute toward a gradually growing literature examining neural mechanisms of mammalian grouping behavior. I'm in good company with researchers leading labs like those of Dr. Annaliese K. Beery, who studies tuco-tucos and voles, and Dr. Michael M. Yartsev, who studies bats.

4.5. *Resistance toward new animal models in neuroscience*

I have been met with both excitement and skepticism about using spiny mice for research. Colleagues reviewing our manuscripts for consideration of publication have been overwhelmingly supportive, as have colleagues at conferences, particularly those at the Society for Behavioral Neuroendocrinology. Yet, I have run into walls time and time again with grant panels. Although I was eventually funded by NSF, I received written feedback such as “why not use prairie voles instead?” At NIH, I also received comments about how I should not use spiny mice and instead use lab mice, prairie voles, or rats. My favorite feedback from an NIH grant review was “the panel is concerned about how findings will translate to rats.” Did you know that the mission of the NIH is to understand the domesticated rat? Further, I was told by a program

officer that "we don't need another social rodent model in our portfolio." I dance the dance, over and over again, in grant proposals. I must justify why I need to use a spiny mouse and cannot simply use a rat or a prairie vole. But I need that justification to be gentle enough so that I don't offend other researchers and their own beloved model system. I've tried tap, jazz, and the waltz. Ongoing grant proposals use interpretive and modern dance — I'm hoping that perhaps I can simply shock reviewers into accepting spiny mice as a viable model for social neuroscience research.

Here's my argument for why spiny mice are a useful organism for sociality research: Most neuroscience studies examining affiliative social behaviors focus on bonding between two individuals in reproductive contexts, such as parent-offspring or mating bonds (Woolley et al., 2004; Young and Wang, 2004; Feldman, 2016). Yet, prior studies indicate that reproductive and non-reproductive contexts are differentially processed in the brain (Lee et al., 2019), and thus we cannot assume that neural circuits underlying reproductive bonding will similarly regulate non-reproductive affiliation. Further, because group living is not part of the life history of the most commonly used laboratory models, it is questionable whether the neural mechanisms that influence social interactions between two individuals in aggressive or reproductive contexts may generalize into an understanding of the complex mechanisms that modulate prosocial interactions with unrelated individuals in large groups like those that characterize human societies. Humans engage in non-reproductive social interactions daily; we refer to such bonds as friendships, acquaintances, or professional interactions. The ability to engage prosocially in *both* reproductive and nonreproductive interactions, particularly in group contexts, is crucial for individual and community health. By harnessing the natural, highly prosocial behavior of spiny mice we can examine how the brain allows individuals to get along in groups and facilitates group cohesion. Additionally, by utilizing a species that forms dynamic social groups, we can identify properties of group interactions, as well as underlying neural mechanisms, that distinguish pivotal changes in group structural dynamics that may lead toward the transition from group cohesion to dissolution. Ultimately, the goal of my research program is to identify brain mechanisms that support living in complex societies, including the neural attributes that promote and detract from cohesion within groups of related and unrelated individuals, something that will become increasingly important to understand as our own societies grow and become more and more complex.

I think it is a compelling argument, but I fear I am either way off base or that the questions are not ones that the neuroscience community finds compelling. Granted (pun intended), there are often other issues with my grant proposals, but it's disconcerting to correct issues and resubmit when the panel and/or the program officer are operating with a baseline preference of "no spiny mice." Biodiversity and comparative approaches are not inherently valued in the biomedical and neuroscience communities in the United States. I'm tired, and I'm too young to be tired. But I will, as have so many others, keep banging my head against that wall. I signed up to try, am lucky enough to have been given the opportunity, and so I will keep trying.

5. Putting it all together

Beyond novel insights into mechanisms of behavior in finches, voles, gerbils, and spiny mice derived from a variety of individual experiments, what else can we learn from the body of research discussed above? Here I discuss a few overarching take-home messages that are, in and of themselves, not new concepts; rather, it is my humble opinion that the work discussed above lends itself well to cogitating broader scientific considerations.

From working with birds, we determined how distinct OT/VP cell groups modulate social behavior (Kelly and Goodson, 2014b). While this research revealed direct contributions of OT/VP cell groups to behavior for the first time, I think it is important to highlight that we observed species differences. As we embed conclusions from these studies into the broader literature, considering species differences becomes all the more important. For example, we found that the BNST VP neuronal population directly promotes aspects of prosocial behavior across finches, with species-specific effects such that this cell group facilitates gregariousness in highly colonial male zebra finches but general affiliative contact in moderately colonial male and female blue waxbills; BNST VP also modulates anxiety in zebra finches but not in blue waxbills (Kelly et al., 2011; Kelly and Goodson, 2013a, 2013b). Further, this neuronal population suppresses aggression in male zebra finches (Kelly and Goodson, 2013b). There are modulatory differences within closely related finch species, but such differences also arise when we look across taxa. Similar studies that knocked down BNST VP production in lab mice found somewhat opposing results to those we found in zebra finches, such that the BNST VP cell group promotes aggressive signaling in male mice but does not influence anxiety in either males or females (Rigney et al., 2022). I think one of the morals of the story here is that the brain is strongly evolutionarily conserved but also incredibly plastic. The VP/OT nonapeptides exhibit evolutionary functional conservation because they modulate social behavior (which is a big, broad term!) across vertebrates (Kelly and Goodson, 2014b). However, unique selective pressures push VP/OT functions in distinct ways to meet the needs of a particular species (Kelly and Ophir, 2015). As a field, we often hope to be able to generalize findings across species, but the environment is crucial for shaping how brains of a species evolve, and in turn, the behavioral ecology that has been selected for as adaptive for a species is then going to be crucial in shaping how a brain develops. Inherent in this complexity are massive amounts of variation. The ultimate goal (hope?) for many behavioral neuroscientists who value a comparative approach is to identify fundamental core principles for how the brain promotes distinct types of social behavior. But if I'm being honest, I think we are far away from achieving that goal. We can only feasibly test so many different species – much to my chagrin, money doesn't grow on trees and wildebeest just won't fit into my lab – and we will always face the challenge of designing complementary behavioral tests to use across multiple species that somehow also account for unique species differences in behavioral ecology. It is extraordinarily difficult to scientifically compare neural function and behavior across species. That said, I absolutely still believe it is a worthwhile pursuit to use a comparative approach in research. Although results may not always generalize across species, we can still gain some predictive value about how distinct environments and selective pressures might shape neural function to achieve specific types of social behavior.

Working with a variety of different species has encouraged me to be a more openminded scientist. We have known for decades that VP/OT modulate basic physiology in addition to behavior (Holmes et al., 2003; Goodson and Thompson, 2010; Alqudah et al., 2022). Yet, we often develop a tendency to label specific brain regions, circuits, and/or cell types as having very specific functions, limiting our exploration into their potentially extensive contributions to behavior. As an example, accumbal OT receptors have primarily been studied in relation to social behavior, specifically bonding between pair bond partners and parents with offspring (Young et al., 2001; Keebaugh et al., 2015; Witchey et al., 2024). However, while we found that these receptors facilitate huddling with strangers in male spiny mice, we also observed that accumbal OT receptors promote feeding behavior (Fricker et al., 2025). OT receptors in the nucleus accumbens have primarily been studied for their role in *social* behavior, but our findings in spiny mice demonstrate that these receptors are also involved in *nonsocial* behaviors. From our work with gerbils, we observed effects of testosterone on behavior that contradict the majority of the literature that shows that testosterone facilitates aggression (Soma, 2006; Carre et al., 2017); yet, when in a non-aggressive context with a pair bond partner or a familiar cagemate/sibling, testosterone promotes huddling in both males and females (Kelly et al., 2022; Kelly and Thompson, 2023)! While testosterone can, and often does, promote aggression, it can also promote prosocial behavior

— *context matters*. Among other non-behavioral processes, testosterone also regulates neuroinflammation (Kanwore et al., 2023; Turniak-Kusy et al., 2024). I'll admit sometimes I slip down the dark abyss of considering how everything in the brain does everything and question whether we really know anything at all. We still just have so much more to learn about the brain. At least there's some job security as a neuroscientist! My occasional existential crisis aside, as scientists we need to be careful not to pigeon-hole ourselves into assuming a particular hormone/neurochemical and/or brain region/circuit/network has specialized and restricted functions. We need to test animals in multiple contexts when possible and keep an open mind when considering which hormones, neurochemicals, and brain regions/circuits may be involved in our behaviors of interest.

Lastly, I think it is important to acknowledge that spiny mice are different. Of course, there are other rodents (i.e., striped mice, naked mole-rats, degus) that share similar characteristics with spiny mice; I am aware that spiny mice are not magical unicorns! However, spiny mice are really quite strange — they are the only mammal known to regenerate entire suites of tissue (Seifert et al., 2012; Seifert and Temple-Smith, 2022), they are the only rodent known to menstruate (Bellofiore et al., 2017), they are precocial (Haughton et al., 2016), and they are unusually prosocial and accept unrelated newcomers into established groups (Cizkova et al., 2011; Fricker and Kelly, 2024). Taken together, it may be difficult to generalize findings from spiny mice to [many] other species. However, by studying a strange organism we can gain insight into how innovation occurs throughout evolution (Adkins-Regan, 1990). With a rapidly changing planet, understanding how innovation arises may become even more pertinent. It is important for us to conduct all kinds of science — science in traditional and non-traditional organisms, science that will generalize, and science that examines rare phenomena.

5.1. Disclaimer

The remainder of this paper deviates from a discussion of my scientific pursuits to date. Read no further if you do not wish to hear any more about my personal musings related to science and education!

6. Changing tides

6.1. My glasses feel heavy on the bridge of my nose

I got into this business as a bright-eyed and bushy-tailed undergraduate student looking for adventure. I certainly gave myself an adventure with the initiative of starting a spiny mouse research program as new faculty. It's not for nothing that the act of writing the section above makes me feel like we have accomplished something. Regardless, as happens to all animals, I'm getting older. I've been watching the shine of research and the novelty of studying sociality wander out to pasture. Yet, I actively run animals through behavioral tests, do perfusions, process tissue, count cells, score behavioral videos, yada yada yada. I still find joy in conducting science. I like to be active and move around. I love the suspense of analyzing data — transitioning from the unknown to the known. And I still enjoy the puzzles — revealing unexpected significant findings that make you question "what does that even mean?!" Yet, with time and through the continual experience of publishing, I have also developed an intolerance for reviewers that, rather than making constructive suggestions to improve the science or clarity of the paper, primarily make stylistic preference suggestions or write a three-page review with their opinions and no concrete requests or suggestions for manuscript changes. I have noticed myself becoming less and less tolerant, as well as less motivated to fight the good fight for pushing the field of neuroscience to value the use of non-traditional organisms. I have developed a more critical scientific eye from being an associate editor for Proceedings of the Royal Society Biological Sciences, a service I enjoy because it forces me to read manuscripts that are far outside my field. Learning about other types of biological research inspires me but also makes me yearn for something new. Am I just a thrill seeker looking for a new adventure? Or has the landscape changed?

6.2. Is the world crumbling around us?

Southern California, not too far from where I grew up, recently experienced some of its most devastating wildfires in recorded history (e.g., January 2025 fires that included the Pacific Palisades fire, Eaton fire, etc.). Hurricane Helene put beautiful Asheville, North Carolina, an inland mountain town, under water in September 2024. Updated climate projections are published frequently by Climate Action Tracker, the National Oceanic and Atmospheric Administration, and the World Meteorological Association. None of the projections are good. There is a 97 % consensus among scientists that humans have accelerated and exacerbated climate change (NASA.gov). I think what saddens me most is that it is not just humans that will suffer the consequences of our actions. How will other animals cope with a changing planet? Is there something we could do to help make at least some species more resilient? Should I conduct such studies? *Can* I conduct research related to climate change? Am I stuck, beholden to the types of scientific questions I've always asked? Do I have the scientific freedom to explore new avenues of research – arguably more pressing, consequential avenues of research? My enthusiasm for the science of sociality is being replaced by a foreboding feeling and concern for the future of our planet. I can't help but think about pillars in our field no longer with us and taken too young — Jim Goodson and Larry Young; life can be too short to feel stuck and not pursue something new. Is it not the millennial way to leave behind what no longer serves you? Maybe I'm thinking of Marie Kondo's advice to discard what no longer sparks joy. Regardless, it feels like the luxurious days of asking questions for the simple sake of curiosity are coming to an end. I feel something akin to guilt for studying a fun topic like social behavior. And, yes, of course there are important aspects to my research. But… is social behavior research in spiny mice really *that* important?

7. The great unknown

7.1. Are we headed toward a sea change?

In 2024, 37.7 % of Americans hold a bachelor's degree or higher (educationdata.org). The most recent data reported by the National Center for Education Statistics (Canafoglia et al., 2006) noted that the number of associate and bachelor's degrees conferred decreased from 2021 to 2022 (The Condition of Education 2024 Annual Report; NCES). College has become extraordinarily expensive. Many Americans argue that college is becoming increasingly irrelevant and does not prepare students for life and work after graduation. However, the number of certificates conferred increased from 2021 to 2022 (The Condition of Education 2024 Annual Report; NCES). Upskilling and microcredentials offered by companies such as Microsoft and Google are in high demand (Levine and Van Pelt, 2021). Academic and educational landscapes, our standard university models of which were built for the Industrial Age, are changing. This is the landscape in which we conduct science. Political landscapes are also changing, and the types of scientific inquiry we prioritize in the United States are likely to change. How much longer will the scientific inquiry of the neural mechanisms underlying sociality, and specifically grouping behavior, be fundable? Somewhat ironically, the very thing I study — getting along in groups – is something we as humans in the United States, and elsewhere, have begun to fail at. Society has become fractured and terrifyingly polarized.

7.2. What's next?

I began with a question about how I got here. I'm living in Georgia

because I loved the problem solving and analytical quest that science allowed me to immerse myself in. Growing up I never had aspirations to live in Indiana or Georgia; I yearned for harsh winters and vast forests! But I've embraced the scientific lifestyle and let it take me places I never thought I'd live. To be a scientist, for me, means chasing the unknown. Science is an adventure. I have been exceedingly fortunate to have been given the opportunity to explore questions of my choosing – questions about what makes animals social. However, there are bigger problems looming on the horizon for science, education, and our planet. For me, they're becoming harder to ignore. My students keep me inspired and it brings me great joy to watch their growth and successes in the lab. However, there's a constant itch in the back of my brain, encouraging me to consider and explore new ventures. Maybe I can somehow contribute to our understanding of the type of physiological plasticity that can make some animals more resilient to our rapidly changing climate. Or perhaps I can help update our country's educational system to reflect the needs of today rather than those of the Industrial era. Regardless of where my professional life takes me, something I've learned from studying animal behavior is that the best thing I can do is remain flexible and adaptable. Perhaps I can learn to channel my inner spiny mouse and regain tolerance so that I can more eloquently cope with the frustrations and struggles that all academics and scientists deal with on a regular basis. And maybe, just maybe, someday I will get to live in the snow again.

CRediT authorship contribution statement

Aubrey M. Kelly: Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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