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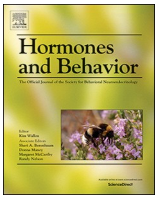

Review article

Frank Beach Award Winner: Lessons from poison frogs on ecological drivers of behavioral diversification

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ABSTRACT

Variation in natural behavior is tightly linked to the ecological resources with which they co-evolved. This review discusses poison frog behavior and neuroendocrinology to illustrate how ecological factors drive diversification of behavior and its underlying neural mechanisms. Poison frogs show tremendous diversity in reproductive strategies that are tightly linked to water resources in their environment. Different species utilize particular pool sizes to rear their offspring, which has selected for sex differences in parental behavior among poison frog species. Tadpole behavior reflects the behavioral diversity of adults, where tadpoles can display social group living or violent aggression and begging behavior, which are all associated with pool size and occupancy. Using this behavioral diversity among poison frog species, we have identified core brain regions, like the hippocampus and preoptic area, as being involved in regulating different aspects of amphibian parental behavior. In contrast to core brain regions, the neuromodulators governing these behaviors seem to be more labile across species. This work exemplifies how comparative studies are a prime experimental system to study how evolution tunes neural circuits that give rise to the diversity of behaviors we observe in the natural world. Finally, this review ends on a more important form of diversity – that of our scientific community – and how community outreach, decolonization of field based science, and inclusion of groups historically excluded from conducting research are needed for the scientific enterprise to transform into something truly beneficial for all members of our society.

RESUMEN

La variación en el comportamiento natural está muy relacionada con los recursos ecológicos con los que coevolucionaron. Esta revisión bibliográfica analiza el comportamiento de las ranas venenosas y la neuroendocrinología para demostrar cómo la ecología influye en la diversificación del comportamiento y los relacionados mecanismos neuronales. Las ranas venenosas tienen diversas estrategias reproductivas basadas en la cantidad de agua en su ambiente. Diferentes especies utilizan charcas de tamaños variables para criar a sus renacuajos, lo cual ha resultado en la evolución de diferencias entre los sexos del comportamiento parental entre especies de ranas venenosas. La diversidad de comportamientos en los adultos se refleja en el comportamiento de sus renacuajos donde algunas especies viven en grupos sociales mientras otras muestran agresión y acciones para solicitar comida. Estos comportamientos de los renacuajos están relacionados con el tamaño y la ocupación del medio acuático. Utilizando esta diversidad de comportamiento entre las especies de ranas venenosas, hemos identificado regiones centrales del cerebro, como el hipocampo y la área preóptica, involucradas en la regulación de comportamientos sociales. En contraste con las regiones centrales del cerebro, los neuromoduladores que gobiernan estos comportamientos parecen ser más lábiles entre especies. Este trabajo ejemplifica cómo los estudios comparativos son fundamentales para entender cómo la sincronización de circuitos nerviosos permiten la diversificación de los comportamientos que observamos en el mundo natural. Finalmente, yo discuto la importancia de diversidad de personas dentro de nuestra comunidad científica y cómo la difusión científica, la descolonización en la ciencia basada en el campo, y la inclusión de grupos históricamente excluidos de la investigación son necesarios para que la empresa científica se transforme en algo benéfico para todos los miembros de nuestra sociedad.

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1. Introduction

> *To know the breeding system is to know the genetic architecture of a species.*
>
> *To know the evolution of a breeding system is to know how evolution works.*
>
> Lewis and Crow, Evolution (1955)

One of the next frontiers in biology is to understand the neural and genetic mechanisms that drive diversity in natural behaviors. This quest holds the key to understanding how new behaviors evolve and to what extent neural mechanisms of behavior are conserved across taxa. From an organismal perspective, behavior and physiology are the substrates of natural and sexual selection, and thus, we will better understand the principles of evolution by determining how these organismal traits diversify. One behavior that is intimately linked with sexual selection is that of parental behavior, where trade-offs between current and future reproduction can explain species differences in reproductive strategies (Royle et al., 2012). Little is known about the neural and genetic mechanisms that govern parental behavior and how species differences in behaviors are specified (Dulac et al., 2014). We know the most about how maternal care is constructed in the brain due to decades of elegant work in laboratory rodents (reviewed in (Numan, 2020)). However, less is known about natural paternal behavior, as there are fewer laboratory animals on which it can be conveniently studied. Moreover, parental behavior can be confounded with many other behaviors, such as pair bonding and territoriality. One of the foundations of neuroethology, or the study of the neural basis of natural behaviors, is that for any given scientific question, there exists an organism (or clade of organisms) best suited to address that question (also known as Krogh's Principle). It was with a question about the evolution of parental behavior and a search for a champion research organism best suited to address that question that I set out to build my own research program.

Amphibians show tremendous diversity in behavior and physiology within and across clades. While completing my dissertation work, I decided that in order to study the neural basis of parental behavior, I needed a research organism that showed diversity in reproductive strategies. This framework would allow the dissection of specific behavioral components that are intertwined in other animals (like paternal care and pair bonding in most mammals). Eventually, I came across the influential work of Kyle Summers on dendrobatid poison frogs, which showed remarkable diversity in parental strategies across closely related species. Similar to mammals, this included female uniparental care and biparental care, but importantly male uniparental care also existed, which does not occur in mammals and is rare in amniotes generally. This was a prime system in which to ask questions about how diversity in reproductive systems evolve because of (1) variation in behavior and physiology between and within species, (2) the relatively simple brain architecture of amphibians, and (3) no studies had been published concerning the brains of poison frogs before, leaving an open niche where I could build my own creative and impactful research program. Luckily, I was able to convince Andrew Murray, Director of the Center for Systems Biology at Harvard University, to let me establish my own lab straight out of my PhD as a Bauer Fellow to study the neuroendocrinology and genomics of behavior in poison frogs. Since then, my lab has studied the evolution of parental behavior and has recently expanded into other social behaviors and the physiology of chemical defense (Fig. 1). In this review, I summarize work from my lab over the past eight years that demonstrates how ecological resources shape neuroendocrine mechanisms of behavior. Along the way, it became apparent that the diversification of poison frog behavioral strategies are tightly coupled to ecological resources in their environment, where evolution selected for neural circuit configurations that promote a variety of behaviors adapted to take advantage of different ecological opportunities.

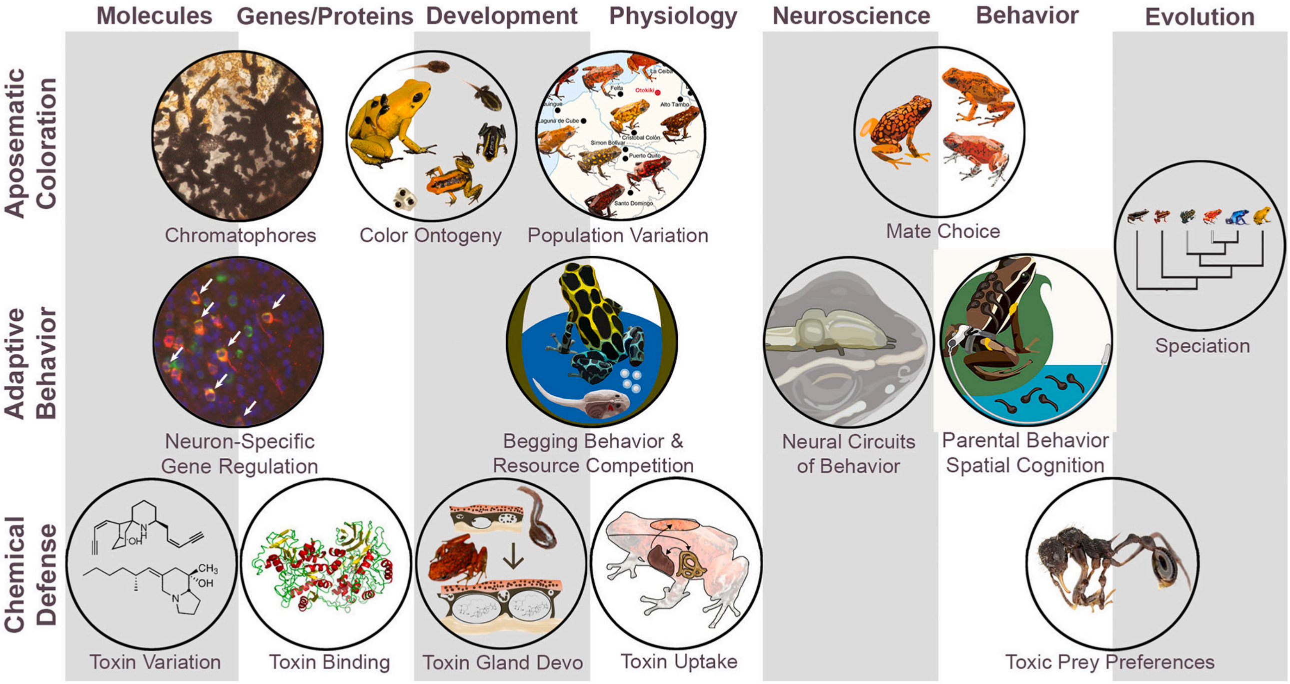

Fig. 1. Poison frogs show variation in physiological and behavioral traits that offer many opportunities to study evolutionary innovations across multiple levels of biological organization. Some (but not all) poison frogs are aposematic (top row), meaning they have bright warning coloration as adults that influence predator and mate interactions. Poison frogs show variation within and among species in various behaviors (middle row), including parental care, exploration, navigation, aggression, and communication. Some (but not all) poison frogs carry chemical defenses in the form of small molecule alkaloids that they sequester from their diet for defense against predation (bottom row).

2. Natural history as a requisite foundation for mechanistic inquiry

Poison frogs in Central and South America (Family Dendrobatidae) arguably display some of the most complex social behaviors among amphibians. Although better known for their bright coloration and toxicity (Summers and Clough, 2001), they also have tremendous diversity in mating systems, parental care, and communication. In the late 1900s, Maureen Donnelly, Heike Pröhl, Kyle Summers, Kentwood Wells, and others described the natural history and reproductive behavior of many dendrobatid poison frog species (Summers, 1992; Summers et al., 2006; Wells, 2010; Weygoldt, 1987). Their decades of field-based research documented variation in reproductive strategies among closely related dendrobatid poison frogs, highlighting complex behavior and social decision-making. Diversity in dendrobatid mating systems and parental care in the context of sexual selection has been extensively reviewed elsewhere (Summers and Tumulty, 2014), but is briefly summarized in this section. I begin with natural history because it is a necessary foundation on which mechanistic studies about the neural basis of natural behaviors are built.

Most poison frog species have long-term territories that are tightly linked to reproductive success (Pröhl, 2005), which is in contrast to lek-based mating systems common in temperate region amphibians. Many dendrobatids are polygynandrous, where both males and females have multiple mating partners (Pröhl and Hödl, 1999; Summers, 1992), while a few display social monogamy and biparental care (Brown et al., 2010). Dendrobatids also vary in their parental care strategies, where male uniparental care is ancestral in the clade but females participate in offspring care in some species (Wells, 2010). Adults are terrestrial and lay their egg clutches in the leaf litter (Fig. 2A). Parents guard the embryos from egg predators during the roughly four weeks of development, where removing parents leads to increased predation (Ringler et al., 2017). After hatching, the tadpoles are aquatic and need to be moved to water for metamorphosis (Fig. 2B). Parents accomplish this task by moving tadpoles piggyback style, where the transporting parent waits for hatched tadpoles to wriggle up onto their back before navigating to a pool of water (Fig. 2C). While tadpole transport is ubiquitous in dendrobatids, some species perform offspring care that extends well beyond tadpole deposition. For most tadpoles, parental care ceases after they are deposited into pools. However, in some species, mothers return to provide trophic unfertilized eggs for the tadpoles to eat (Fig. 2D). This unusual egg-provisioning behavior has evolved twice within the family (genera *Oophaga* (Brust, 1993) and some *Ranitomeya* species (Summers et al., 2008)). In these egg-feeding species, parent-offspring communication has evolved, where tadpoles beg caregivers for food with vigorous vibrations that are distinct from swimming behavior. Tadpole begging behavior is required for egg deposition by females, although what components of these signals are important is not well understood.

In today's scientific forum of precision genetic technologies, many researchers underestimate the importance of natural history and painstaking hours of field observations in building solid foundations for more mechanistic inquiry that maintains ecological relevance. Field work over several decades by Walter Hödl, Heike Pröhl, Kyle Summers, Kentwood Wells, and others led to the detailed catalog of the tremendous diversity in poison frog behavior. As of the early 2010s, when I was completing graduate school, no studies had investigated the neural or hormonal basis of these complex behaviors seen across the poison frog clade. It is on the shoulders of these giants that I decided to lay the foundations of my own research program and become the first lab focusing on the neural basis of social behavior in poison frogs and how ecological factors drive diversification of neuroendocrine mechanisms. After nearly a decade, we are beginning to better understand how evolution and ecology tune conserved neural circuits to give rise to the behavioral diversity observed by naturalists for many decades.

3. Ecological resources and the evolution of reproductive strategies

The availability of resources, including mates, food, and offspring rearing sites, is linked to the diversification of behavioral strategies across many species. For example, the availability of potential mates within a population is a key factor in predicting sex and species differences in adult social behavior (Kvarnemo and Ahnesjo, 1996). Territorial defense can also be linked to nutritional resources and lead to the evolution and maintenance of pair bonding, as shown in pair bonding butterflyfishes that jointly defend their main diet of coral (Nowicki et al., 2018). The utilization of ecological resources for offspring rearing can also lead to new behavioral traits. For example, mosquito disease vector strains that prefer biting humans over animals likely evolved this olfactory preference due to their reproductive need of standing water pools for egg laying and reliable water pools are only

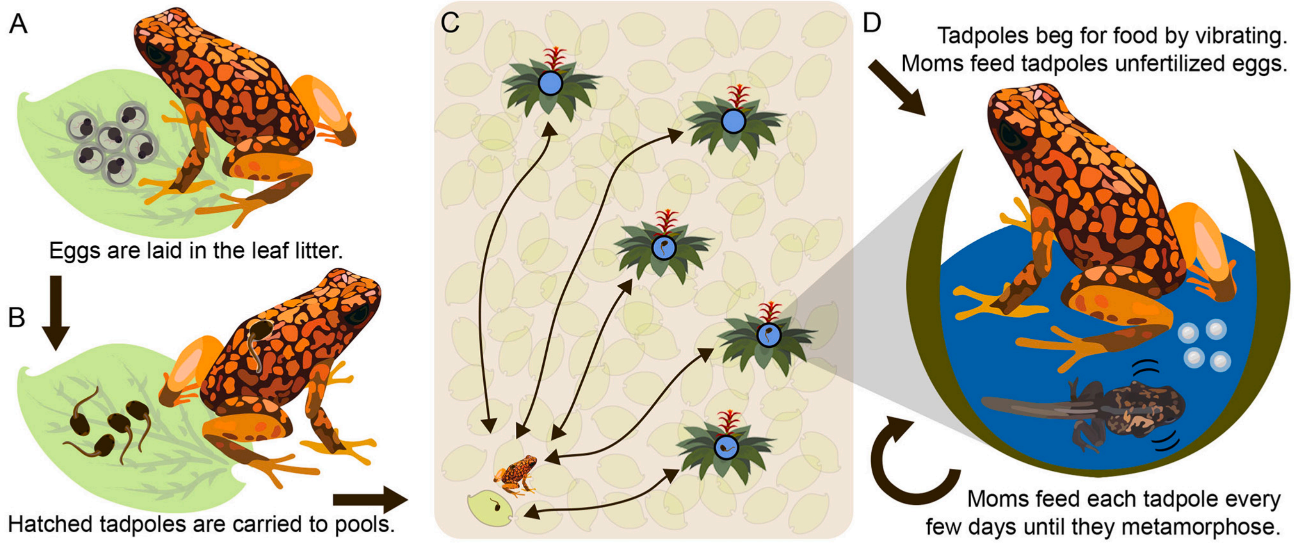

Fig. 2. Parental care in poison frogs. (A) Dendrobatid frogs are terrestrial and lay their egg clutches in the leaf litter. (B) Hatched tadpoles are aquatic and must be carried to water by their caregiver. (C) Parents must navigate to pools in which to place their tadpoles. (D) In a few dendrobatid species, mothers return to tadpole pools to feed offspring trophic unfertilized eggs every few days until metamorphosis.

associated with human households in dry seasons (Rose et al., 2020). In dendrobatid poison frogs, the diversification of parental care strategies has been linked to both sexual conflict over tadpole cannibalism and water pool size, availability, and nutritional content.

Poison frogs show uncommonly diverse sex differences in reproductive strategies. While male uniparental care is ancestral in the clade, both biparental and female uniparental care strategies have evolved (Fig. 3A). While males transport tadpoles in most species, for example in the Brilliant-thighed poison frog (*Allobates femoralis*) and the Dyeing poison frog (*Dendrobates tinctorius*), both parents will transport tadpoles in the biparental and monogamous *R. imitator*, while only females transport tadpoles in the Diablito frog (*Oophaga sylvatica*). Males tend to transport tadpoles in groups and place them together in larger pools (Fig. 3B). In species where females participate in care, tadpoles are placed in pools contained in plants (phytotelmata), where both predators and nutritional content are lower, but the reproductive resource itself can be relatively rare (Donnelly, 1989; Poelman and Dicke, 2008). In these species, mothers perform egg provisioning behavior throughout tadpole development, feeding trophic unfertilized eggs to their offspring. This egg feeding represents a physiological production of food analogous to mammalian lactation or avian crop milk (Oftedal, 2012). Work by Kyle Summers and Jason Brown suggests that female parental care evolved with the use of small pools with poor nutritional resources (Brown et al., 2010; Summers and Earn, 1999). Tadpoles are usually placed individually (rather than as a group) in these resource-poor pools, and have evolved begging behavior to solicit mothers for egg meals and/or fierce cannibalism to defend their nurseries from other tadpoles. Thus, the movement into a novel ecological niche of phytotelmata selected for female parental care in the form of egg provisioning, allowing tadpoles to develop in nutrient poor nurseries. Although there is an established connection between ecological resources and behavior, we have just now begun to understand how ecology can drive evolutionary innovations in behavior from neuroendocrine perspective.

4. Neuroendocrine basis of sex differences and plasticity in parental care

Sex differences in parental care across closely related species sets the stage for identifying key brain regions that promote parental behavior in both males and females. Comparing species that vary in behavior is valuable because it allows us to ask what generalizable mechanisms facilitate behavior versus species-specific mechanisms. In the context of parental care, this can be difficult to accomplish in mammalian species, where males that provide offspring care are typically biparental and pair bond to their partner, making parental care and pair bonding difficult to disentangle in the brain. A series of studies in my lab set out to utilize species differences in parental behavior, as well as behavioral plasticity within a species, to identify general neuroendocrine principles of parental behavior.

The first study that formed the justification for establishing my entire research program focused on determining the neural signature of tadpole transport across three species that differ in parental care strategies (Fig. 4A (Fischer and Roland et al., 2019b)): male uniparental (*D. tinctorius*), female uniparental (*O. sylvatica*), and biparental (*R. imitator*). Specifically, tadpole-transporting parents and their non-transporting partners were captured, and we examined patterns of neural activation across several brain regions that have conserved roles in mediating social behavior across vertebrates (O'Connell and Hofmann, 2011). Our main approach for asking this question was using phosphorylated ribosomes as a proxy for neural activity to identify brain regions and neuroendocrine factors that may be involved in tadpole

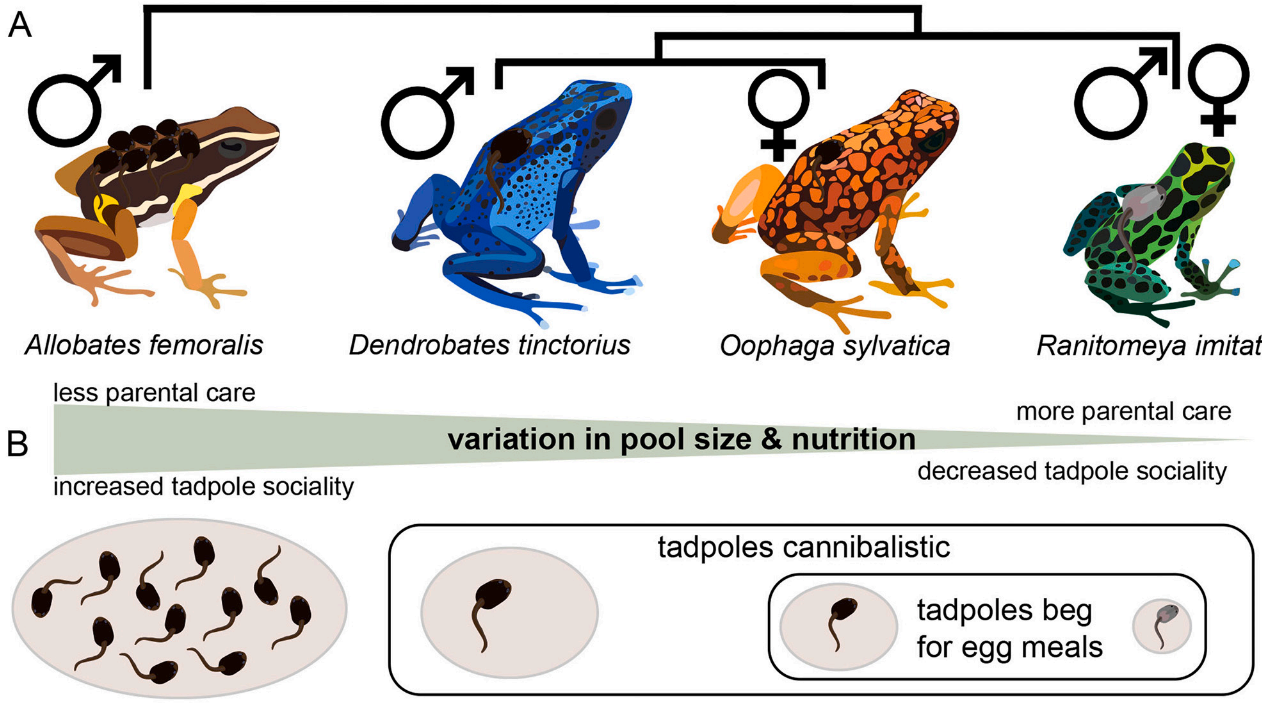

Fig. 3. Variation in reproductive strategies and tadpole behavior are linked to differences in ecological resources. (A) Dendrobatid poison frog species vary in reproductive strategies. Male uniparental care is ancestral in the clade, where males care for egg clutches and transport tadpoles to water pools. Some species are female uniparental where females perform tadpole transport and feed developing tadpoles trophic unfertilized eggs. Other species are monogamous and biparental, where parents coordinate territory defense and offspring care. (B) Species differences in parental care strategies are mirrored by species differences in tadpole behavior. Tadpoles that are transported into large pools as a group are non-aggressive (left). Species that distribute their tadpoles into smaller pools usually carry them one at a time. These tadpoles are typically aggresive cannibals and will consume other tadpoles. In species where females are involved in parental care (right), each tadpole is deposited into separate tiny pools of water, typically contained in plants, where mothers return to feed them. Egg provisioning has led to the evolution of begging behavior in tadpoles, where tadpoles dance for their egg meals.

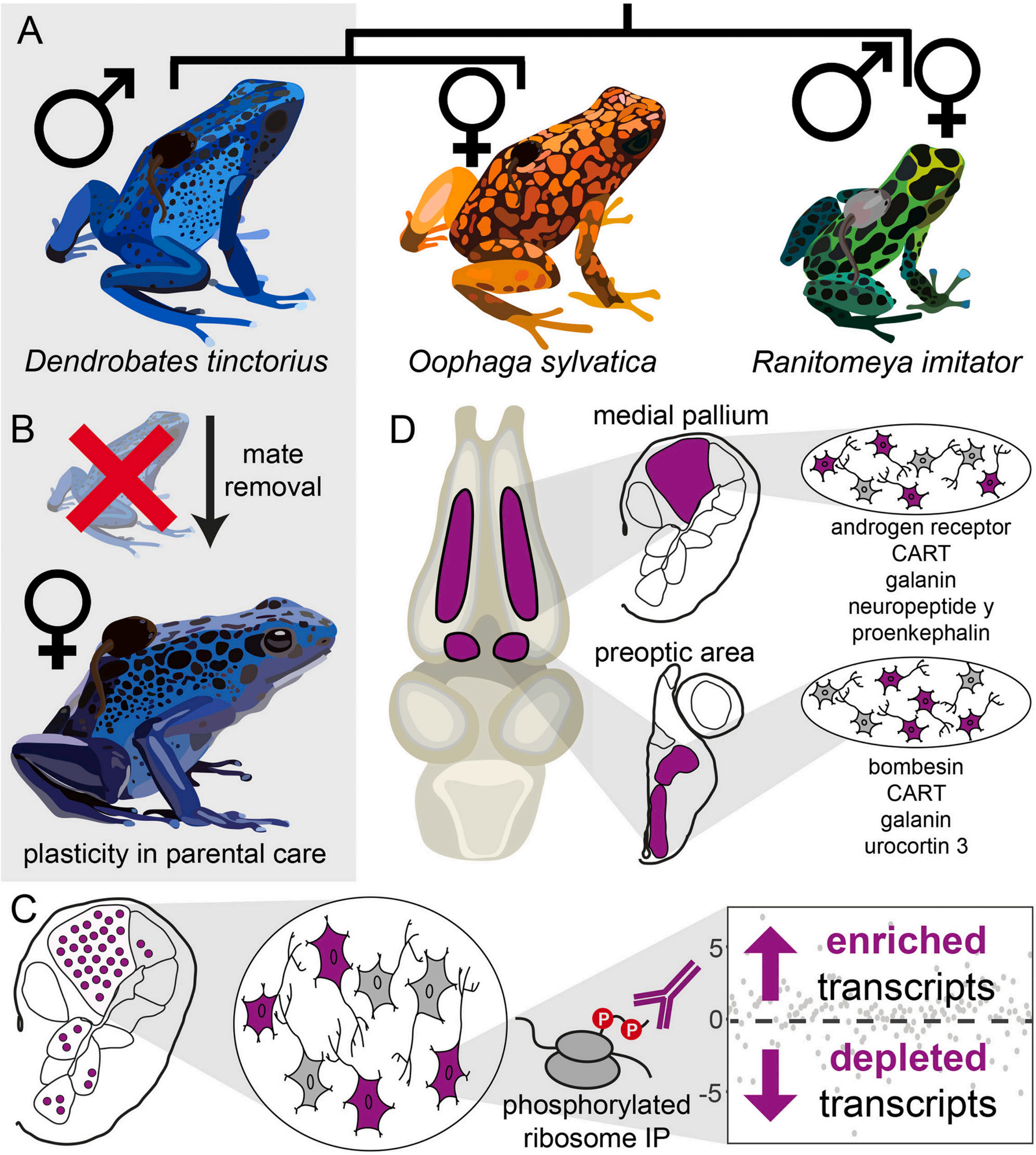

Fig. 4. Within and between species comparisons used to identify core brain regions involved in parental care. (A) Poison frogs show species differences in which parent transports tadpoles to water, including male uniparental care (*Dendrobates tinctorius*), female uniparental care (*Oophaga sylvatica*), and biparental care (*Ranitomeya imitator*). (B) In some species, there is plasticity in parental behavior, where the sex that does not normally provide offspring care will do so if the other parent disappears. (C) To identify brain regions with increased neural activation associated with offspring transportation, we used immunohistochemical detection of phosphorylated ribosomes. After identifying brain regions with more active neurons during tadpole transport, we used a phosphorylated ribosome immunoprecipitation followed by sequencing to identify transcripts enriched or depleted in activated neurons compared to total RNA input. (D) In both between and within species comparisons, our studies highlighted two brain regions (purple), the medial pallium (amphibian hippocampus) and preoptic area, that had higher neural activity in frogs transporting tadpoles compared to controls, regardless of sex. Sequencing of active neurons in those brain regions highlighted several neuromodulators that may regulate parental behavior, but many still need to be tested to confirm their functional role. Together, this research identified core brain regions involved in tadpole transport and revealed that the neural circuitry for parental care exists in both sexes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

transportation (Fig. 4C). This approach highlighted two brain regions that were consistently active during tadpole transport behavior (Fig. 4D): the medial pallium (the amphibian hippocampus) and preoptic area. The location of water pools within the environment is a spatial memory task linked to reproductive success (Pašukonis et al., 2016), providing a direct link between an ecological resource and brain function. Hippocampal plasticity is also linked to maternal care in rodents (reviewed in (Leuner et al., 2010)), and thus hippocampal activity may reflect a conserved role for spatial memory in parenting strategies across many taxa. The other brain region consistently active during tadpole transport in males and females is the preoptic area, which has long been associated with parental behavior (and many other social behaviors) across vertebrates, including mammals (Kuroda and Numan, 2014; Lee and Brown, 2002), birds (Ruscio and Adkins-Regan, 2004), fish (O'Connell et al., 2012), and now amphibians. This work also suggests there are common brain regions that promote parental care in males and females.

Although some poison frog species are considered male uniparental, there are laboratory and field studies documenting plasticity in parental care, where the sex that typically does not perform tadpole transport will do so if the other parent is removed to ensure offspring survival. For example, *A. femoralis* tadpoles are usually transported by males, but females will transport tadpoles if the male disappears (Ringler et al., 2015). We used this plasticity feature to examine the neural mechanisms of tadpole transport in *D. tinctorius*, a typically male uniparental care species where females occasionally perform tadpole transport in the laboratory (Fig. 4B). By comparing females that transported their tadpoles after the male was removed to females that did not perform this task, we were able to confirm the medial pallium and preoptic area as core nodes important for tadpole transport behavior (Fischer and O'Connell, 2020), similar to our comparison of multiple species (Fischer and Roland et al., 2019b). More broadly, this study suggests that the neural circuity for parental care exists in both males and females, but only one sex typically performs the task. The social or environmental triggers of this parental care circuitry are unknown and represent a future area of valuable research.

After identifying the brain regions associated with tadpole transport, we then asked which neuroendocrine factors may be facilitating tadpole transport behavior. We molecularly profiled neurons active during tadpole transport using phosphoTRAP and found several neuroendocrine-related genes that were enriched or depleted in each brain region (Fig. 4D). For example, the androgen receptor was enriched in active neurons in the medial pallium, which may point to a role for androgen-mediated enhancement of spatial cognition, which is well described in mammals (Jones and Watson, 2005). Common neuromodulators expressed in neurons active during tadpole transport in both brain regions were galanin and CART (cocaine- and amphetamine-regulated transcript). Work by Catherine Dulac's laboratory has identified galanin neurons in the preoptic area as necessary for parental behavior in male and female mice (Wu et al., 2014). Follow-up work then delineated the galanin circuit for parental care by teasing apart which aspects of rodent parental behavior are associated with distinct galanin-positive projections within the brain (Kohl et al., 2018). Despite the promising related literature in mice, we only observed galanin-positive neuronal activation within the preoptic area during tadpole transport in biparental *R. imitator*, but not *D. tinctorius* and *O. sylvatica*. In male uniparental fish (Tripp et al., 2020) and rats (Bloch et al., 1993), galanin is associated with courtship and copulation, rather than paternal care. Comparing across vertebrates, these studies suggest the role of galanin in regulating social behavior varies with life history traits in a complex manner that warrants further investigation.

The molecular signatures associated with tadpole transport behavior highlighted several neuromodulators that are typically associated with feeding behavior. Specifically, we found that bombesin, galanin, POMC (pro-opiomelanocortin), CART, and urocortin transcripts were enriched in neurons active during tadpole transport, while NPY (neuropeptide Y) transcripts were depleted (suggesting decreased activity of NPY-positive cells during tadpole transport). The arcuate nucleus of the hypothalamus controls feeding behavior and appetite in mammals, where neurons co-expressing NPY and AgRP (Agouti-Related Peptide) stimulate appetite while neurons co-expressing POMC and CART suppress appetite (reviewed in (Yeo and Heisler, 2012)). Galanin enhances appetite (Corwin et al., 1993) and has been linked to parental behavior in laboratory mice (Wu et al., 2014) and in *R. imitator* frogs. Urocotins (I, II, and III) generally suppress food intake in rodents (reviewed in (Stengel and Taché, 2014)), but have also been linked to parental

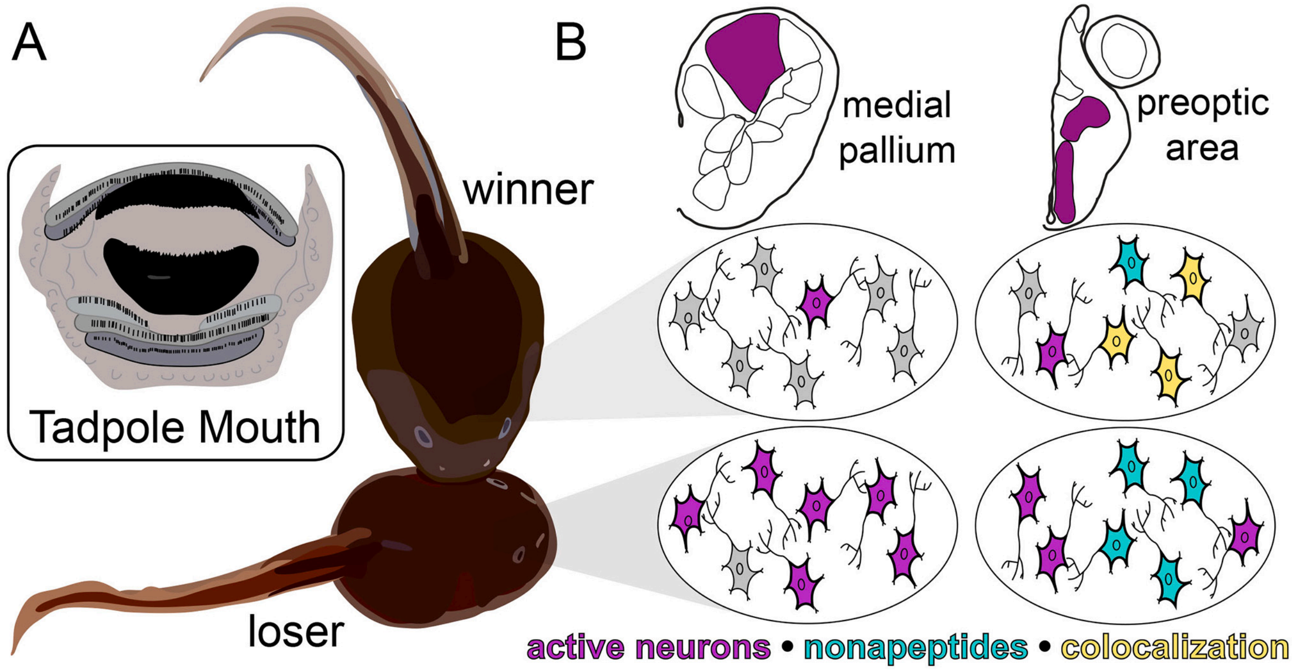

Fig. 5. Some dendrobatid tadpoles are cannibalistic and display fierce aggression. (A) Cannibalistic tadpoles have sharp beaks and many rows of needle-like teeth (inset). In behavioral trials, winners and losers are quickly established. (B) Neural activity (purple) is higher in the medial pallium and the preoptic area in losers compared to winners and non-fighting control tadpoles (bottom row). Although losers have higher activity in the preoptic area, winners have higher activity in nonapeptidergic (oxytocin and vasopressin, blue) neurons. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

behavior. Urocortin II induces spontaneous parental behavior in prairie voles (*Microtus ochrogaster*, (Samuel et al., 2008)), and urocortin III neurons promote infanticide in mice (Autry et al., n.d.), which involves an adult eating pups in a natural setting (Svare and Mann, 1981). In many species, parental behavior often involves the modification of feeding circuitry, whether this means eating more to physiologically produce food as in lactation or foraging to feed offspring rather than oneself. Given the enrichment of feeding related hypothalamic neuromodulators in our parental care studies, I previously proposed that the evolution of parental behavior involves the modification of neural feeding circuitry, either to decrease feeding behavior to avoid eating offspring or increase feeding behavior to gain nutrients that are allocated to offspring (Fischer and O'Connell, 2017). Indeed, poison frogs will sometimes cannibalize eggs and tadpoles (Ringler et al., 2017), suggesting modulating foraging and feeding behavior is important in caring for one's own offspring.

Together, this body of work utilized species differences in which sex cares for offspring, as well as within-species parental flexibility, to identify core brain regions and neuromodulators involved in tadpole transport. These brain regions and neuromodulators are also important for parental behavior in other species (Numan, 2020) and suggests that, although parental care evolved independently across vertebrates (Dulac et al., 2014; Royle et al., 2012), similar circuits govern these behaviors (Fischer and O'Connell, 2018). Whether tuning neural circuits that govern interactions with ecological resources, like feeding/foraging behavior and finding water resources, is a general principle underlying diversification of parental behavior remains an open question. This work also allowed us to identify species or sex-specific patterns of neural activation in tadpole transport, whose role in specific components of parental care are not known. One of the next frontiers in this field of research is to leverage comparative work across species to understand how the tuning of conserved neural circuits, like those governing feeding behavior, changes across species to drive natural variation in parental behavior.

5. Ecological resources and the evolution of tadpole aggression

Variation in poison frog tadpole behavior reflects the behavioral diversity seen in adults. Tadpoles can vary in sociality, where some live in large mixed-parentage groups while others will cannibalize any tadpole intruder whether they are related or not (Gray et al., 2009). Cannibalistic species have specialized adaptations to enhance fight

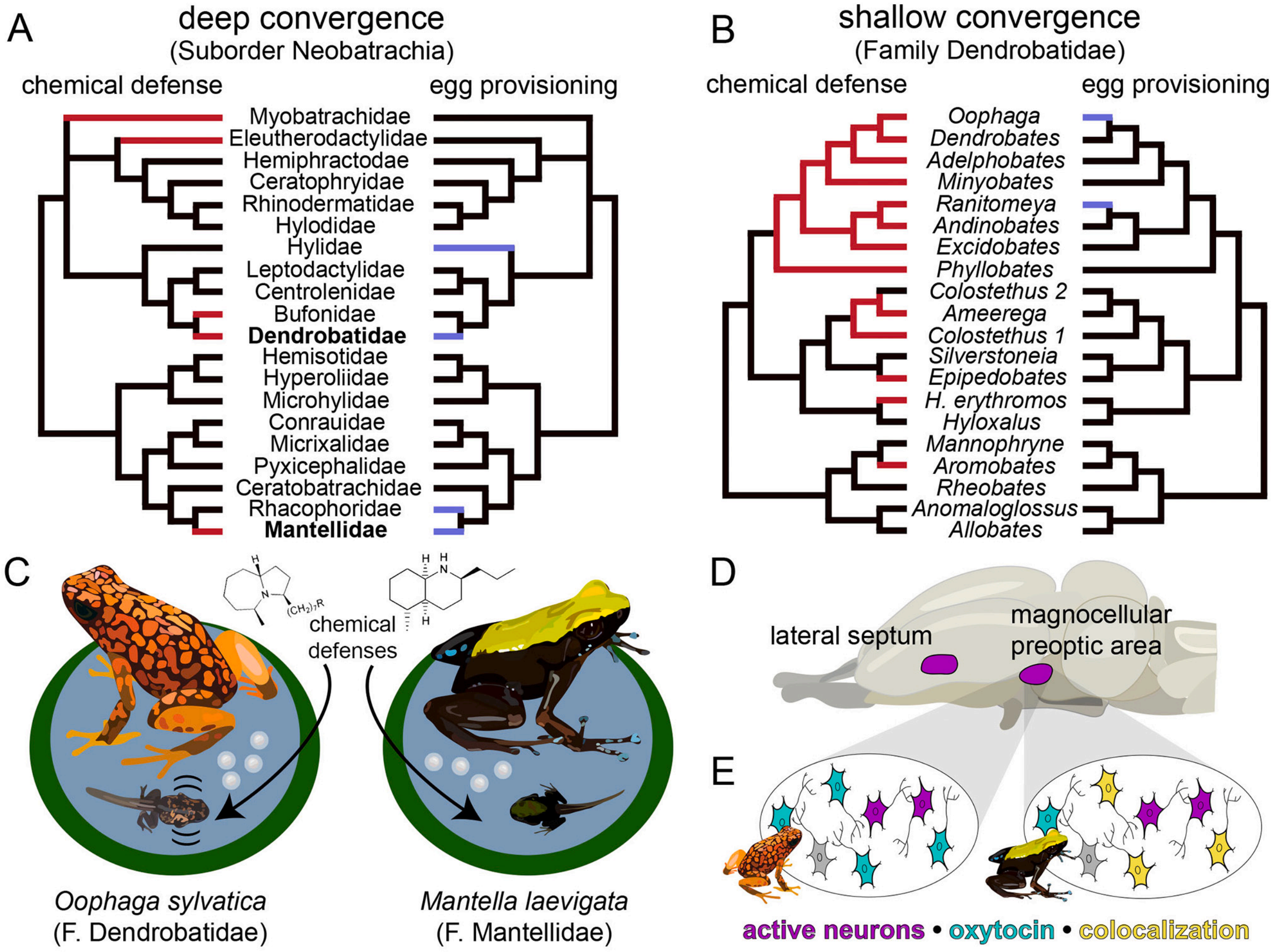

Fig. 6. Evolutionary innovations in maternal behavior and correlation with eco-physiological traits. Chemical defenses (red, left phylogenies) and egg provisioning behavior (blue, right phylogenies) have independently evolved in many (A) families within Neobatrachia (true frogs) as well as (B) within the Family Dendrobatidae. In some species, chemical defenses and egg provisioning behavior co-occur. (C) *Oophaga sylvatica* (left, F. Dendrobatidae) and *Mantella laevigata* (right, F. Mantellidae) last shared a common ancestor around 140 million years ago, and yet both species sequester chemical defenses that are passed to their tadpoles through trophic unfertilized eggs. (D) In both species, nursing females have more active neurons in the lateral septum and magnocellular preoptic area (purple) compared to non-nursing controls. (E) Despite both species having increased neural activity in the magnocellular preoptic area, only *M. laevigata* have more active oxytocin neurons (blue) during nursing behavior, whereas *O. sylvatica* oxytocin neurons were less active during nursing. This suggests that although similar brain regions may contribute to behavior, different molecular mechanisms may be responsible. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

outcome, including a mouth with many rows of needle-like teeth and a sharp keratinized beak (Fig. 5A inset). The propensity to display aggression is reflected in how many tadpoles are transported at a time by the parent, where group-transported tadpoles are less aggressive than those that are transported singly (Fig. 3). Small or medium sized pools can be resource-limiting, which sometimes leads to males depositing younger tadpoles in pools with older tadpoles (Gray et al., 2009; Rojas, 2014). This provisioning of younger offspring to the older ones comes at a cost to female reproductive success, where the tadpoles are likely to have the same fathers, but different mothers (Summers, 1990). This sexual conflict is hypothesized to have driven the evolution of female tadpole transport in some dendrobatid species (Summers and Tumulty, 2014). A study manipulating food levels in *O. pumilio* tadpoles found that aggression towards conspecifics did not change, suggesting aggression serves to defend the water pool as a resource rather than to obtain nutrition (Dugas et al., 2016). It is currently unclear whether parental decisions of nursery pool size or nutritional content shaped juvenile behavior or if cannibalistic tadpoles selected for parental behaviors that separate offspring into different pools.

Hormones have long been tied to aggressive behavior, with testosterone and its aromatization into estradiol playing critical roles (Trainor et al., 2017). However, the neuroendocrine basis of aggression in juveniles is less clear, as many mammalian young display more play fighting than violent aggression when sex steroid hormones are not yet abundant (Takahashi and Lore, 1983). We have examined the neural basis of aggression in *D. tinctorius* tadpoles, which are cannibalistic and will readily fight conspecifics in the wild (Rojas, 2014). We staged encounters between size-matched tadpoles and compared neural activity of tadpoles that did not engage in a fight (controls) to tadpoles that either won or lost a fight (Fig. 5A (Fischer et al., 2020)). We found increased neural activity in the medial pallium and preoptic area of loser tadpoles (Fig. 5B). These two brain regions were also associated with tadpole transport behavior in adult poison frog parents (Fig. 4), suggesting a broad role for these two brain regions in amphibian social behavior. Research into the neural basis of juvenile play behavior has highlighted an important role for the nonapeptide vasopressin, where administration of vasopressin receptor antagonists reduces play behavior in male rats (Cheng and Delville, 2009; Veenema et al., 2013). We next examined neural activity within nonapeptide cells and found that winners had increased activity of nonapeptidergic neurons in the preoptic area compared to losers and controls (Fig. 5B). Although pharmacological tests are still needed to confirm a functional role for vasopressin specifically, this preliminary study suggests similar mechanisms of violent aggression in tadpoles and juvenile play behavior in mammals. More generally, studying species differences in aggression represents a promising direction to better understand violent aggression in pre-pubertal animals.

6. Evolutionary innovations in parent-offspring interactions

A major question in evolutionary biology is how novel phenotypes arise. As behavior is the substrate on which natural selection acts, studying behavioral innovations, like pair bonding or parental care, allows us to better understand how evolution reshapes existing gene regulatory networks or neural circuits to produce novel behavioral traits. Determining whether the underlying mechanisms driving new phenotypes arise through convergent or distinct pathways depends on the timescale at which these behaviors are being compared. For example, maternal care is present in all mammals and the circuitry underlying mother-offspring bonding is thought to lay the groundwork for the evolution of adult pair bonding given the overlap of these neural circuits and modulators (Numan and Young, 2016). However, the neural basis of pair bonding in other animals seems to be different from mammals, for example, in butterflyfishes that do not display parental care (Nowicki et al., 2017). Research across various taxa emphasizes how phylogenetic relatedness is an important consideration when studying behavioral evolution, where more closely related species may be more likely to have similar neuroendocrine mechanisms underlying behavior than more evolutionarily distant animals (Fischer et al., 2019a). Understanding the extent to which the independent evolution of behavioral strategies rely on similar or distinct molecular mechanisms is an important future direction for the field of behavioral neuroendocrinology, but requires comparative work outside of the more common model systems in neuroscience.

Poison frogs have evolved acquired chemical defenses and parental care at deep (wide evolutionary distances) and shallow (clades with more recent speciation) levels of the frog phylogeny. Comparing species at deep and shallow convergence timescales is valuable for understanding how the repeatability of mechanisms that underlie convergent evolution is influenced by shared ancestry. For example, frogs in the Dendrobatidae and Mantellidae families have evolved both acquired chemical defenses and egg provisioning behavior and occupy two separate branches of the frog phylogeny sharing their last common ancestor roughly 140 million years ago (Fig. 6A). Within the Dendrobatidae family, chemical defenses have evolved four times independently across genera and only species that are chemically defended have evolved egg provisioning behavior (Fig. 6B). Given the overlap of chemical defenses and maternal egg provisioning behavior, we conducted a study to test the hypothesis that the independent evolution of egg provisioning behavior relied on similar ecological and neural mechanisms (Fischer and Roland et al., 2019c). We compared both chemical defenses and signatures of neural activity associated with egg provisioning behavior in *Oophaga sylvatica* and *Mantella laevigata* by collecting nursing mothers and their tadpoles in the field (in Ecuador and Madagascar, respectively). We found that in both species, mothers provisioned tadpoles with alkaloids through trophic eggs, which provides tadpoles with chemical defenses much earlier than non-egg feeding poison frog species (Fig. 6C), whose tadpoles only acquire alkaloid chemical defenses when they become terrestrial after metamorphosis. The provisioning of alkaloids to tadpoles had been demonstrated in *O. pumilio* by Jennifer Stynoski, who showed that maternally-provisioned chemical defenses protect tadpoles from predation (Stynoski et al., 2014a, 2014b). Together, this work suggests that the provisioning of chemical defenses may be another adaptive advantage of egg provisioning in poison frogs, maintaining this costly behavioral strategy. Moreover, as mothers (and their tadpoles) derive these chemical defenses from their arthropod diet, it is another example of how ecology contributes to behavioral diversity.

As the independent evolution of egg provisioning behavior seems to have shared defensive and nutritive benefits for offspring, we next asked if the neural mechanisms contributing to nursing behavior were similar across wide evolutionary distances. We compared females who were observed provisioning eggs to their tadpoles to control females that were not performing this behavior. We found common signatures of increased neural activity in the lateral septum and magnocellular preoptic area in nursing mothers in both species (Fig. 6D), suggesting these brain regions are important for facilitating egg provisioning behavior. Although the function of the amphibian lateral septum is unknown, the mammalian lateral septum is involved in social memory (Dantzer et al., 1988). Social memory is likely linked to egg provisioning in amphibians as mothers must remember both where their tadpoles are located. The magnocellular preoptic area was also more active in nursing mothers, and given its association with tadpole transport behavior (Fig. 4B, (Fischer and Roland et al., 2019b)), the preoptic area seems to be a critical node for distinct components of parental behavior. This reflects studies in mammals where the preoptic area is important for various aspects of both male and female parental behavior (Brown et al., 2017; Jacobson et al., 1980; Kohl et al., 2018; Numan, 1974). As oxytocin is important for maternal behavior in mammals, and the magnocellular preoptic area is the location of oxytocin (also known as mesotocin) neurons in the amphibian brain, we next examined neural activity specifically within oxytocin-positive neurons in both species. We found that oxytocin neurons were more active in nursing *M. laevigata*, but seemed to be inhibited during nursing behavior in *O. sylvatica* (Fig. 6E). In summary, this study found that similar ecological benefits and the same brain regions may facilitate unique behaviors that evolved in evolutionarily distant taxa. However, evolving new behaviors may involve alternative mechanistic solutions, where different cell types or gene regulatory networks are recruited to produce analogous behaviors. The extent to which alternative or similar mechanistic solutions are implemented in the evolution of novel behaviors remains an open question.

7. Summary of how ecology shapes neural circuits in poison frogs

Studying poison frogs has allowed us to address fundamental questions in behavioral neuroendocrinology that are otherwise inaccessible in other vertebrate research organisms. For example, we have studied the neural basis of male uniparental behavior, which is not present in mammals, to better understand how paternal care is distinct from pair bonding in the brain (Fig. 4) and highlighted core brain regions that are involved in parental behavior in many vertebrates. Similarly, laboratory rodent pups do not display violent aggression like tadpoles (Fig. 5), which provides an opportunity to understand how violent aggression is elicited in a juvenile brain without the circulating sex steroid hormones of adulthood. We also used the convergent evolution of maternal behavior in dendrobatids and mantellids (Fig. 6) to ask questions about the repeatability of behavioral evolution or whether there are many mechanistic solutions to promoting maternal behavior in the brain. As maternal behavior is ancestral and ubiquitous among mammals, such a question can only be asked in non-mammalian species. Convergent evolution in general is an excellent framework in which to map genotype to behavioral phenotype, as it provides natural repeated measures to identify general emergent properties of neural systems versus species specific mechanisms, both of which are valuable findings (Gallant and O'Connell, 2020). In both our poison frog parental care studies, the brain regions active during parental care were similar among frog species and also in other vertebrates. The hippocampus and preoptic area were both found to be involved in poison frog parental behavior and aggression. These brain regions are involved in many social behaviors across vertebrates and highlight the need for understanding how specific cell types and their projection patterns govern social behavior. This cell type specific perspective will be valuable, as we found the cellular mechanisms that govern parental behavior in different species seem to be evolutionarily flexible. Identifying neural components that are generalizable versus labile opens many avenues for understanding how evolution tunes existing neural circuits across animals to produce analogous behaviors. Furthermore, many of the behavioral adaptations discussed here co-evolved with ecological limitations (e.g. nutrition) and opportunities (e.g. availability and size of offspring-rearing sites). How ecology has shaped the neural circuits that govern nutritional tuning of behavior or the preferences of individuals for specific ecological resources remains an open question.

8. Shaping our community values while pursuing our passions

A senior colleague told me that it is not very often that we get a soapbox on which to stand on, so I should use this Beach Award opportunity to communicate what I really care about. While I am quite certain this advice was referring to my scientific pursuits, the aspects of my career that I am most passionate about are social justice issues that require reshaping our communities to be more equitable. A more open discussion on the social capital of science and who does and does not benefit from its institutionalization is becoming more common. Extraordinary people are stepping up with their voices on how to reshape our community for the better, for example, with advice on how to make scientific conferences more equitable for caregivers by Rebecca Calisi Rodriguez (Calisi and a Working Group of Mothers in Science, 2018), historical insights into the contributions of diverse scientists studying animal behavior by Danielle Lee (Lee, 2020), and how to fight anti-Black racism and white supremacy in the fields of ecology and evolution (Schell et al., 2020). The longer I am in science the more I realize that my privilege as a white woman has elevated me to where I am today and that the institutionalized power of the privileged is preventing equity in the science. Thus, my soapbox ends on our social justice responsibilities to broaden participation in science through outreach, decolonize field-based science, and increase inclusion within academia.

When sitting down to write National Science Foundation (NSF) grants, many principal investigators bemoan the Broader Impacts section – a required plan to disseminate research findings to the public and/or make efforts to include underrepresented groups in their research. Broader Impacts is the first section of NSF grants that I write, as this is one of the few places where we can design community engagement strategies to make academic science more inclusive and communicate to the public why studying poison frog neuroendocrinology is a worthwhile investment. The field of behavioral neuroendocrinology is sometimes faced with skepticism from the public as to why precious tax dollars are spent investigating topics that have no obvious link to developing therapeutics for human disease. As recipients of taxpayer funds through federal grants, we have a responsibility to communicate the importance of our research to the public so that they become stakeholders in our discoveries (McNie et al., 2016). An excellent starting point is put forth by Bik et al. (2015), who provide a set of 10 rules for effective outreach that includes how to establish and evaluate outreach programs and why this process is valuable to researchers and society as a whole (Bik et al., 2015). Establishing collaborations with educators is extremely important for ensuring outreach is measurably meaningful to the community (Varner, 2014) and not merely as a photo or resume opportunity for scientists. However, there are clear institutional impediments to outreach, as many academic units do not value these activities and there are strong gender differences in who participates (Andrews et al., 2005; Ecklund et al., 2012). Support for our research programs is greatly facilitated when the public values our research and communicates this to their governmental representatives – the importance of this positive feedback loop cannot be overstated.

Ecologically-relevant research is grounded in natural history, where studying organisms in their natural habitat provides a necessary foundation on which to build more mechanistic inquiry. When field research is conducted outside of one's home institution, it expands the communities to which we are accountable. Scientific colonialism is deeply rooted in the genocide and exploitation of indigenous peoples (Smith, 2012). An example from my own field involves poison frog chemical defenses, where a chemical isolated from an endemic Ecuadorian frog was patented as a novel analgesic by chemists at the National Institutes of Health in the United States (Spande et al., 1997). This bioprospecting left a scar of mistrust and fear of further exploitation for many decades (Angerer, 2011). It takes time to build trust and authentic collaborations with local people, which should be reciprocally beneficial to all parties. This includes collaboratively designing a study to ensure outcomes are aligned with local community needs, continuing with investments in local science training and education, and culminating in an outcome that appropriately credits local collaborators. General evidence for scientific colonialism can be seen in our natural history museums (Sheets-Pyenson, 1987) and in scientific publications (Dahdouh-Guebas et al., 2003). For example, only 35% of recent publications (2010 – 2020) with field work focusing on poison frog behavior and chemical ecology included a local collaborator, with most publications excluding local people taking place in former or current colonies. Finally, neoimperialism has made English the language of science, which creates inequities in who can access scientific literature and careers. For example, English proficiency is correlated with high socioeconomic status in some countries, allowing certain students to access science easier than their peers (Ramírez-Castañeda, 2020). While having a common scientific language is important, we are responsible for crossing language barriers constructed by neocolonialism if we are conducting field work in regions that speak a different language. Scientific colonialism shaped much of what we know about the natural world and is still active today. Our field of study benefited from scientific colonialism, so consider teaching in your classroom and laboratory about the role of imperialism in science and how Western scientific practices limit our understanding of the natural world. These decolonization efforts are critical to making transformative progress in science, maintaining research ethics, and ensuring our research output is beneficial for all people (Baker et al., 2019).

For science to be beneficial for society, the composition of our scientific community must reflect our societal diversity. The professoriate and academia generally is far less diverse than the general population. Currently in the United States, Black, Hispanic and female professors are underrepresented in the professoriate, while white and Asian professors are overrepresented (Li and Koedel, 2017). This exclusion of underrepresented groups in academic science is perpetuated by occupational inheritance of parental cultural capital, where professors are likely to be children of advanced degree holders themselves (Breen and Jonsson, 2005). This disparity is important because students look to their professors as role models, where students most benefit from both gender and racial/ethic matches (Egalite and Kisida, 2018). Let us consider community colleges in the United States, as they are more diverse than four year universities and I care deeply about this population, having attended community college myself as a low-income student. Roughly 45% of low-income students attend community colleges (Berkner et al., 2008), due to tuition savings, proximity to home, and flexibility in schedules while working full-time. Over 44% of Black students, 53% Native American students, and 56% Hispanic students begin their education at community colleges (Ma and Baum, 2016). Despite 80% of community college students reporting the intent to earn a bachelor's degree, only 14% end up doing so (Jenkins and Fink, 2016), as transfer students report experiencing attitudes from professors and peers implying they do not belong at four-year institutions because of ethnicity, age, and socioeconomic status (Reyes, 2011). However, performance gaps of minority students at community colleges can close by up to 50% if professors more closely resemble their students (Fairlie et al., 2011). A major path to recruitment into science for underrepresented groups is summer research internship programs (Packard, 2012), although there are very few opportunities for community college students to participate. Given community colleges are where nearly half of all underrepresented groups in STEM begin their higher education, we should place more emphasis on their recruitment and inclusion in the scientific community.

Group diversity generates innovation in science (Nielsen et al., 2017), and more importantly, there are social justice concerns when excluding certain groups of people from the scientific enterprise. Thus, it has become clear that retention is equally important to recruitment efforts. Indeed, demographically underrepresented students are more innovative than their majority peers, although their contributions are more likely to be discounted (Hofstra et al., 2020). This so-called Diversity-Innovation Paradox may partially explain an underrepresentation of minorities in prestigious awards and leadership positions and reflects the institutionalized bias of academic scientists. As another example of bias, retention in STEM is adversely affected when students feel stereotype threat, or risk displaying attributes that align with negative stereotypes about their social group, and the magnitude of this effect can be either positively or negatively tuned by peer interactions (Meador, 2018). The recruitment and retention of historically excluded groups in science is not a new problem, as there is an entire field of literature dedicated to the topic, where effective strategies have already been laid out, including mentorship, research experiences, financial support, and instructional reform (Tsui, 2007). However, if there is a body of literature with a clear roadmap for effectives strategies to diversify STEM, why are certain groups still excluded from practicing science? Joseph Graves, the first African American to earn a PhD in evolutionary biology in the United States, writes, “If this profession is really serious about increasing the participation of African Americans in this field, it must first examine its own cultural and implicit biases” (Graves, 2019). We have been failing to retain diverse scientists because we expect them to simply fit into the system once they are recruited. Since the academic system is founded on and perpetuates institutionalized racism and discrimination, it is the majority that must reflect on their own biases and change the system itself into one that creates an inclusive environment for diverse scientists to flourish.

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Declaration of competing interest

None.

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