ORIGINAL PAPER

The evolution of parental care, aposematism and color diversity in Neotropical poison frogs

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This Special Issue demonstrates the breadth of evolutionary ecology research occurring on Neotropical poison frogs (Dendrobatidae). It also draws attention to the incredible diversity of the poison frogs themselves (phenotypic, behavioral and taxonomic diversity) and this group's potential for research programs focusing on speciation, the evolution of toxicity, color pattern diversity, Müllerian and Batesian mimicry, sexual selection, mating systems and parental care. This Special Issue focused on two key research foci in the field of evolutionary ecology: (1) Understanding the interplay between ecology and the evolution of parental care and (2) Elucidating the ecological factors contributing to the evolution of toxicity, aposematism and color pattern diversity. In this paper, I summarize the major findings of studies presented in this Special Issue.

Understanding the interplay between ecology and the evolution of parental care

Parent poison frogs transport and subsequently deposit their tadpoles in pools of water. The evolutionary transition from terrestrial to smaller arboreal phytotelmata for tadpole deposition is thought to be driven by a reduction in competition and predation associated with smaller tadpole nurseries. This transition is considered a key evolutionary innovation, allowing access to relatively unexploited resources and facilitating the evolution of many novel breeding strategies. To date, there are only a few empirical examples in dendrobatids to support this hypothesis (Weygoldt 1980; Caldwell 1997; Brown et al. 2010). Field experimentation by McKeon and Summers (2013) present a more complete picture of the interactions between the natural history of *Allobates femoralis* and the tadpole predators present. Their results suggest that pool size, the presence of predatory insects and inter-actions between predators (and indirect effects on tadpoles) influence larval deposition in *A. femoralis*.

  Previous research on *Ranitomeya* species, a genus distantly related to *Allobates*, has demonstrated that adults also assess multiple aspects of reproductive resources to

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maximize the success of their offspring. For example, Schulte et al. (2011) demonstrated that, in addition to visual assessment, adult *Ranitomeya* species assess chemical cues specific to common predators present in phytotelmata. For some *Ranitomeya* species this decision is not limited to tadpoles, but also embryos that are deposited in phytotelmata and then transported to individual pools after hatching. In one of these species, *R. amazonica*, Poelman et al. (2013) demonstrated that parents make separate decisions regarding the quality of reproductive resources for tadpole and embryo depositions; with small resource-limited pools being used for egg deposition (where food is not important) and larger resource-rich pools for their tadpoles.

Recent studies have also demonstrated that dendrobatid species exhibit behavioral plasticity in deposition strategies associated with seasonal variation. Poelman and Dicke (2007) observed that populations of *R. amazonica* in French Guiana deposit embryos and tadpoles in separate phytotelmata during the rainy season. At the onset of the dry season, as the result of increased desiccation risk, the males change their strategy and embryos are deposited in pools containing their tadpoles (despite the abundance of vacant reproductive resources). The newly deposited embryos are then consumed by the resident tadpoles, potentially speeding up their development and reducing desiccation risks. Schulte and Lötters (2013) provide a second example of temporal variation in parental care in *Ranitomeya*. They studied a Peruvian population of *R. variabilis*, the sister species to *R. amazonica* (see Brown et al. 2011), and demonstrated that adults avoid depositing their tadpoles in pools containing other congeneric tadpoles during the rainy season. Upon entering the dry season, males begin depositing newly hatched tadpoles in pools containing their older tadpoles that are immediately cannibalized in effort to accelerate development before pools dry. These behaviors represent a potential transition from male-only care to bi-parental care. Alternatively, the existence of this behavior in two deeply diverged sister species suggest that this feeding behavior is stable and that the transition to biparental care is either particularly complicated, or for some species, may not be the optimal parenting strategy. These results also demonstrate that poison frogs assess multiple factors and actively make decisions to maximize the success of their offspring. This adaptive plasticity in behavior does not appear to be restricted to species with increased parental care (i.e., biparental care), but is present in distantly related lineages of poison frogs, supporting the idea that competition, predation and reproductive resource quality have long been a major force in the evolution of poison frogs (see Summers and McKeon 2004 for an overview).

Ecological factors contributing to toxicity, aposematism and color diversity

The effect of parasite infection and its influence on sexual selection and corresponding sexual signals has received little attention in poison frogs. A Special Issue paper by Pröhl et al. (2013) provides evidence that the level of parasite load in a Costa Rican population of *O. pumilio* had minimal impact on their coloration, color brightness, behavior and acoustic parameters. This research opens the door for future research focusing on the relationships between habitat quality, parasite loads and sexual signals, and the effect of these factors on the long-term reproductive success and survivorship of poison frogs.

In poison frogs, the availability of toxic prey and level of diet speciation have been linked to aposematism (Santos et al. 2003; Saporito et al. 2007; Maan and Cummings 2012; Henga et al. 2012). Here Rudh (2013) further demonstrated that conspicuousness of populations was positively correlated with larger body size in *O. pumilio*. These results

suggest that the physical size of the signal also contribute to the effectiveness of aposematic coloration (or alternatively, crypsis).

Factors that contribute to phenotypic variation in aposematic species are poorly understood, however it is thought that interactions between natural selection and sexual selection may be responsible. In many cases, phenotypic diversity is polytypic, with divergent phenotypes being geographically isolated (*e.g.* in *R. imitator*), however some cases aposematic species are polymorphic. Richards-Zawacki et al. (2013) used mark and recapture surveys and clay models to measure predation pressures on two sympatric morphs of *O. pumilio*. Their results revealed no evidence of differential survival, even in light of marked differences in coloration (red and yellow). These results suggest that, at least in some populations, generalized aposematic signals are effective in predator deterrence or alternatively, multiple signals can be effective, even with increased predation rates due predator learning. These results are consistent with results on a closely related species, *O. histrionica*, occurring in Andean Colombia. Amézquita et al. (2013) combined two measures of predation rates, a field method using variable clay models reflecting several geographically isolated morphs of *O. histrionica* and a cryptic control, and a laboratory experiment using chicks and images of the same populations. Their field results also support the conclusion that predators generalize aposematic signals in variable species. Conversely in their laboratory experiments the chicks did not generalize their avoidances. The authors conclude that this suggests chicks are not appropriate proxies for the behavior of predators in the field. Both field studies contrast with previous studies demonstrating differential adaptation to local predator communities resulting in reduced survival of novel phenotypes (Noonan and Comeault 2009; Chouteau and Angers 2011; Hegna et al. 2012).

A Special Issue study on a population of *Dendrobates tinctorius* observed differences among sexes in color pattern and microhabitat use (Rojas et al. 2013). This study presented one of the first examples of sexual dimorphism in color pattern in an aposematic poison frog, consisting of small differences in the proportion of bright coloration on the dorsum and limbs. The authors conclude these differences are the result of synergy between female preferences for brighter males and increased exposure of males to predators due to differences in microhabitat use (favoring selection for conspicuousness in males). This study suggests that male aposematic poison frogs may be under stronger natural selection than females—a topic worthy of future inquiry in other populations and species.

The evolution of phenotype diversity in *O. pumilio*, and other dendrobatids, represents a complex interplay between natural and sexual selection. In the Bocas del Toro populations, it appears that natural selection maintains a largely 'honest' aposematic signal of population toxicity (Maan and Cummings 2012). In this Special Issue, Cummings and Crothers (2013) build upon previous results, using an irritant assay on mice as a proxy for general toxicity. Their results support the existence of room for variation in warning coloration via sexual selection in some populations. They concluded that variation in color patterns across the archipelago may in fact be "ecologically neutral" as long as a sufficient level of conspicuousness maintains aposematic signal (Ruxton et al. 2004).

Demographic history is thought to be important in the evolution of coloration of *O. pumilio*, with small effective population sizes in Bocas del Toro populations presumed to be a major factor in initiating phenotypic divergence (e.g. Summers et al. 1997). In contrast, recent demographic and genetic modeling on southern populations of *O. pumilio* (including Bocas del Toro populations) suggest that a recent population expansion, not isolation on islands, may be central to the color diversification of this species (Gehara et al. 2013). The authors conclude that rapid genetic drift occurred at the edge of expanding populations and initiated phenotypic divergence, then female mate choice caused rapid

fixation and further divergence. These results are consistent with the observed genetic and phenotypic diversity in this species, with polytypic populations being restricted to the south of the species' range (but not restricted to island populations). These simulations also revealed that the intensity of female mate choice required for phenotypic divergence is positively correlated with the level of population stability—with small or expanding populations experiencing faster gene coalescence times than declining or large stable populations (Excoffier et al. 2009; Arenas et al. 2012; Gehara et al. 2013).

Conclusions

The relationship between the form of parental care and the mating system within a species is an issue of fundamental importance to understanding the ecology and evolution of animal breeding systems. Despite decades of research, the specific ecological factors that drive the evolution of parental care remain a subject of debate, particularly in the case of vertebrates. Recent research on poison frogs provides compelling evidence for the crucial roles of specific ecological factors in the evolution of parental care (e.g. Brown et al. 2010; McKeon and Summers 2013; Poelman et al. 2013; Schulte and Lötters 2013).

The evolutionary relationship between natural and sexual selection and its role in the origin and maintenance of phenotypic variation has been a central question in evolutionary biology. In the past decade researchers have made considerable progress elucidating the key factors underlying the evolution of coloration in several species of poison frogs (e.g. research on *O. pumilio* and *R. imitator*: Summers et al. 1997; Symula et al. 2001; Maan and Cummings 2012; Richards-Zawacki et al. 2012). In the near future, due to advances in genomics and bioinformatics, we will begin to unravel the explicit genetics underlying coloration and pattern. However, even in light of these advances (current and future), poison frog researchers have a lot to learn about the specific factors underlying the interactions between sexual and natural selection and their role in promoting phenotypic diversity, population divergence, speciation and the evolution of Müllerian mimicry in aposematic species. Lastly, placing these results in context with other model systems used to study the evolution color diversity (i.e., guppies and cichlid fishes, *Heliconius* butterflies and side-blotched lizards) will contribute to our understanding of the major contributing factors and processes.

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