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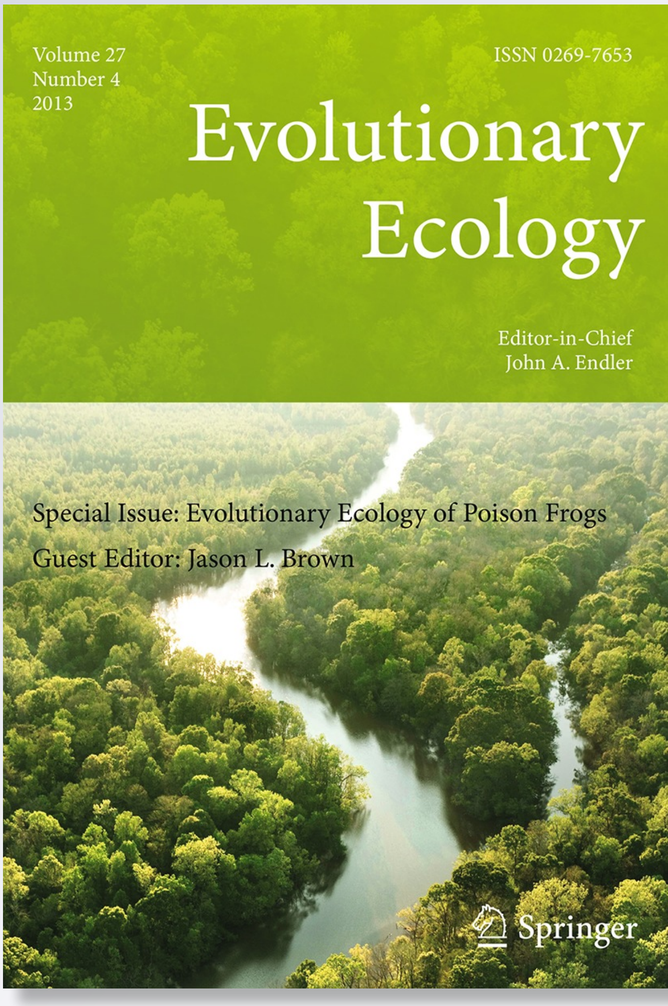

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ORIGINAL PAPER

Neotropical poison frogs: evolution's guide to parenting, fashion and communication in a dynamic world

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Introduction

Few groups of amphibians invoke such an abiding fascination as the Neotropical poison frogs (Dendrobatidae). For many people, these tiny, often brightly-colored frogs serve as ambassadors to the Neotropical rainforests. For some, they may conjure up images of Chóco Indians clothed in loin cloths, armed with blowgun darts coated in highly toxic alkaloids secreted by poison frogs, hunting in misty rainforests. Though slightly romanticized, these caricatures get to the core of why these frogs have been the focus of over 350 scientific studies: poison frogs are toxic and many alert predators of their toxicity through bright warning coloration (aposematism).

The evolutionary history of Neotropical poison frogs (Dendrobatidae) is the result of a dynamic interaction between ecology and evolution—their evolutionary ecology. Each species' history was shaped by their local ecology (i.e., toxicity and abundance of prey, population structures and sizes, predation, larval and adult competition) and varying intensities of natural and sexual selection (including sexual conflict). Each diverging lineage, constrained by their own genetic inheritance and phylogenetic inertia, traveled a unique path that led to the astonishing diversity we observe today.

This Special Issue of *Evolutionary Ecology* summarizes multiple avenues of research related to the Second Symposium on "Poison Frog Ecology, Evolution and Behavior" at the 7th World Congress of Herpetology. This issue focuses on two key research foci in evolutionary ecology: (1) Understanding the interplay between the ecology and the evolution of parental care and (2) Elucidating the ecological factors contributing to the evolution of toxicity, aposematism and color pattern diversity.

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Fig. 1 Phenotypic variation of *Oophaga pumilio*. Localities: (all in Bocas del Toro, Panama unless specified). *Top left* (*clockwise*): Buena Esperanza, Róbalo (Quebrada Cascaje), Guarumo, *top right* (*top–bottom*): Aguacate (Cerro Brucho), Bribri (Puerto Viejo de Talamanca, Talamanca, Costa Rica), Fila Carbon, Isla San Cristóbal, Isla San Cristóbal, Isla Solarte, Rambala, *bottom right* (*right–left*): Aguacate (Buena Esperanza), Rambala, Solarte, Guabo, *bottom left* (*bottom–top*): Guarumo, Guarumo, Isla Colón, Isla Pastores, Isla Popa, Isla 'Posa Dos'. *center images* (*top–bottom*): Isla Bastimentos, "Playa Larga" Isla Bastimentos, Aguacate (Tierra Oscura). Photos from Thomas Ostrowski

Parenting: interplay between ecology and the evolution of parental care

Anuran parents assess a wide array of environmental factors and reproductive resources as they strive to maximize the success of their offspring. In addition, they may provide care to ensure performance and survival of their offspring. In poison frogs, the ecological characteristics of breeding sites appear to underlie transitions in parental care. For example, in some *Ranitomeya* species a single ecological factor, the use of small pools for tadpole deposition, drove the evolution of biparental care and genetic and social monogamy (Brown et al 2010). This transition was mediated by a reduction in tadpole competition and cannibalism associated with smaller tadpole nurseries. Despite considerable research on this topic (e.g. Summers and Amos 1997; Poelman and Dicke 2007; Brown et al 2010), the specific steps in the evolution of increased parental care are not well understood. Recent studies, including several in this Special Issue, have focused on characterizing the preferences, abilities and mechanisms of parental assessment of reproductive resources (for both tadpole and embryo deposition) (See McKeon and Summers 2013; Poelman et al 2013; Schulte and Lötters 2013). A detailed understanding of these factors can provide considerable insight into the specific pathways and causes of the evolution of arboreal phytotelmata use and increased parental care.

Fashion and communication: ecological factors contributing to toxicity, aposematism and color variation

In poison frogs, the availability of toxic prey and nature of dietary specialization have been linked to aposematism (Santos et al 2003). In most cases, selection for aposematism should conserve warning signals throughout a species' range. It is thought that a single warning display not only enhances discrimination by educated predators, but also improves learning and memory retention with respect to the toxicity of defended animals (Poulton 1890; Ruxton et al 2004). However many toxic dendrobatid species exhibit considerable variation in phenotype (see Fig. 1 showing variation in *Oophaga pumilio*; Lötters et al 2007). In some instances, female mate choice is thought to play a major role in color and pattern diversification (e.g. Summers et al 1997). However many other poison frog species fit traditional expectations and their phenotypes are largely conserved. The intensities of and interaction between natural and sexual section in populations are likely the result of a species' local ecology, level of sexual conflict, demography and the molecular basis of coloration (see Table 1 for details; e.g., Summers et al 1997; Maan and Cummings 2012; Martin et al 2012; Gehara et al 2013). Variations in each of these factors are likely responsible for the dramatic levels of phenotypic variation, or in other cases lack of variation, in contemporary poison frog species. For Special Issue papers focusing on various facets of this topic, see: Amézquita et al 2013; Cummings and Crothers 2013; Gehara et al 2013; Pröhl et al 2013; Richards-Zawacki et al 2013; Rojas et al 2013; Rudh 2013.

Table 1 Major factors affecting natural and sexual selection on color and pattern in poison frogs

Factors	Effects	Specific types/examples
Ecological	Changes the intensity of natural selection for aposematic coloration	The spatial and temporal variation of prey toxicity and predators, predator abundance and number of predators driving aposematic selection, co-occurrence of other aposematic species
Sexual conflict, mating system, type of parental care	Influences intensity of sexual selection via female mate choice	In species where females control a large part of parental care, males and their sexual signals can be subject to higher intensities of female mate choice
Population genetics and historical demography	Influences the intensity of selection (both natural and sexual) required for phenotypic diversification. Also effects the intensity and influence of genetic drift	Level of historical introgression between sister taxa, spatial and temporal variation of demes, effective population sizes, population densities, gene flow among populations
Molecular	Controls the ability of a population to respond to selection	Cost of synthesis of aposematic signal, sensory biases and genetics of coloration, including: controllers of gene expression, number and diversity of genes, location of loci on chromosomes, distribution of loci among chromosomes and amount of epistasis

For additional information, see Figure 1 in Cummings and Crothers (2013) in this Special Issue for a visual depiction of the relationship between natural and sexual selection on the evolution of coloration and toxicity

Spatial variation of color and pattern

For the dendrobatid community it is worth clarifying a common, widespread misunderstanding of the word 'polymorphism'. In population genetics and evolutionary genetics, polymorphism refers specifically to discontinuous variation *within* populations (Ruxton et al 2004). Often poison frogs display discontinuous phenotypic variation throughout their distribution, with limited variation within populations—these species are polytypic (Mayr 1963). For example, in the Bocas del Toro, Panama island populations of *Oophaga pumilio* each possess a unique morph. In this area, *Oophaga pumilio* is polytypic with exception to the polymorphic populations on Isla Bastimentos where two discrete morphs co-occur. If variation is continuous within a population, or clinal across geography, this is simply spatial phenotypic variation or population phenotypic variation, respectively (not polymorphic and polytypic, Mayr 1963).

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