

# **Early development and the honesty of aposematic signals in a poison frog**

Submitted by

**Eric Enrique Flores De Gracia**

to the University of Exeter as a thesis for the degree of

Doctor of Philosophy in Biological Sciences

12<sup>th</sup> November 2012

This thesis is available for Library use on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgement.

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature: .....



Juvenile of *Dendrobates auratus* at the study site in Santa Fe de Veraguas, Panama. Photo: Eric Flores, 2009.

## Abstract.

---

The causes and consequences of variation in aposematic signals during immature stages are not clearly understood. This thesis explores the effects of early environment on the expression of aposematic signals in the green and black poison frog (*Dendrobates auratus*), and the consequences of variation in such components in the wild. It also explores how aposematic expression relates to levels of chemical defences in immature froglets. Embryos and larvae of poison frogs in the genus *Dendrobates* are known to be darkly pigmented. This thesis reports for the first time polymorphism in egg pigmentation in *D. auratus* and ontogenetic colour change through development reverting to a normally pigmented phenotype; however whether this pigmentation results from constraints or has adaptive consequences remains unclear. Evidence on how immature individuals allocate resources to growth and warning signalling is scarce. Experimental results in this thesis show that food supply during early environment affected body size and signal luminance in post-metamorphic froglets. Therefore the relative importance of these traits in relation to predation risk was further tested, using artificial prey in a field experiment. The results indicated that rates of attack by birds correlated negatively with body size, and on the contrary survival of artificial prey was independent of signal luminance. I therefore tested the hypothesis that in the wild larger, relatively well-nourished juvenile frogs are chemically better defended. I found that in fact larger juveniles are at a selective advantage conferred by their greater foraging efficiency and their superior levels of chemical defences. Overall, these results shows plasticity in aposematic traits in relation to early environmental nutrition in *D. auratus*; and suggests that acquiring large body size and similar integument colour as to adults are key determinants for survival during the early stages of their terrestrial life.

## Acknowledgements

First thank to my family for their virtual company and support trough these years, in special to my mother, I love you. Many thanks to my supervisors Jonathan Blount and Allen Moore for allocating time and constant advice regarding experimental design, field work and manuscripts preparation and revisions, and also to John Hunt for his crystal clear advice as mentor. I am in debt with Martin Stevens for his big support with the modelling of vision systems, a core part of this thesis. I am also grateful to John Endler and Hannah Rowland for their suggestions and discussions on experimental designs and manuscripts. Thank you to Christopher Mitchell who did a brilliant and professional work with biochemistry analyses. Thanks to James Roper for encouraging me to do a PhD and for his solid and opportune advice, obrigado! Thanks to Luitgard Shwendenmann for her recommendations and support. In Panama Nelva Alvarado and Benjamín Name deposited their confidence on me to start this journey for what I am indebted. I would like to give special thanks to people and friends that contribute in different ways to achieve this task: Rachel Page, Janalee Caldwell, Tom Spande, Rodolfo Contreras, Luis Ureña, Alfonso Ramallo, Carlos Bonilla, Jean Baptiste Saulnier, Iker Vaquero-Alba, Alfredo Attisano, Alberto Pinto, Joseph Macedonia, Iva Fukova and Pilar Velásquez.

Many thanks to the following people that made the impossible tasks possible for me in the field: Edgar Toribio, Eliécer Pineda, Caroline Filmore, Paul Budgent, Carolyn Loeb, Georgia Croxford, Leesther Vásquez, Joelbin de la Cruz, Melva Olmos, Katherine Rodríguez, Víctor Bravo, Hortencio Palma, Jonathan

González, Luis Abrego, Carlos Abrego, and of course the Toribio's Family and the people in Alto del Pito in Santa Fe.

I have to recognise the support from the SENACYT-IFARHU program in Panama who awarded me a PhD scholarship and in special to SENACYT for the research grant that funded my second field season. The School of Biology at the University of Panama in Veraguas, ANAM-Veraguas, ANAM-UNARGEN, and ICGES helped me to solve key technical problems while in Panama, many thanks.

# Table of Contents

Abstract.	iii
Acknowledgements.....	iv
Table of Contents .....	vi
List of Tables.....	viii
List of Figures .....	ix
List of Equations .....	xii
Chapter 1. General Introduction.....	1
1.1. Aposematic signals in relation to early developmental conditions .....	1
1.2. Phenotypic plasticity and aposematic signals.....	3
1.3. Physiological constraints and expression of aposematic signals .....	4
1.4. Design of aposematic signals and predators response.....	5
1.5. Honest signalling in aposematic species.....	7
1.6. Study species and field site .....	10
1.7. Aims and structure of the thesis.....	12
Chapter 2. Unusual whitish eggs in the poison frog <i>Dendrobates auratus</i> Girard, 1855.....	15
2.1. Abstract.....	15
2.2. Introduction .....	16
2.3. Methods.....	17
2.4. Results.....	19
2.5. Discussion.....	22
Chapter 3. Diet, development and the optimisation of warning signals in post-metamorphic green and black poison frogs .....	26
3.1. Abstract.....	26
3.2. Introduction .....	27
3.3. Methods.....	33
3.4. Results.....	49
3.5. Discussion.....	59
3.6. Appendices: Supplementary Methods and Results .....	68
Chapter 4. Body size but not warning signal luminance influences predation risk in recently metamorphosed poison frogs.....	89
4.1. Abstract.....	89
4.2. Introduction .....	90

4.3.	Methods.....	95
4.4.	Results.....	104
4.5.	Discussion.....	107
4.6.	Appendices: Supplementary Methods and Results.....	114
Chapter 5.	Relationships amongst aposematic signals, foraging capacity and toxic defences: behavioural observations of juveniles of a poison frog in the wild.....	124
5.1.	Abstract.....	124
5.2.	Introduction.....	125
5.3.	Methods.....	128
5.4.	Results.....	139
5.5.	Discussion.....	144
5.6.	Appendices: Supplementary information.....	152
Chapter 6.	General discussion.....	155
6.1.	Phenotypic plasticity of aposematic traits early in life.....	155
6.2.	Honesty and automimicry of the aposematic signal.....	158
6.3.	Concluding remarks.....	162
References		164