Introduction

Natural selection is extremely powerful, and arguably the most interesting force in the Universe. It is also one of the most difficult to investigate, because we can view only a snapshot, and therefore must work backwards to understand how it functions, and by what rules. We could not do that but for one saving grace: in a general sense, natural selection repeats itself with some frequency. The resulting analogous patterns in nature allow us to evaluate which components of a system are integral to its evolution, and which are incidental. Thus, the investigation of components of reproductive success, or ecological limitation, only make sense in light of those parameters that are common between the current study and others like it.

Such scientific investigations carry a special burden, however. Historical events are necessarily individual in nature, and thus do not meet the criteria necessary for rigorous statistical interpretation. As such, investigators of evolutionary patterns of convergence need to be especially careful not to over-interpret their conclusions, as no degree of precision can be placed on their level of certainty. This dissertation focuses on the previously unstudied side of an apparently extraordinary convergence.

Species in the family of neotropical poison frogs, Dendrobatidae, are known for the lipophilic alkaloids in their skin, attendant aposematic coloration, and a diverse array of complex behavior. They are small, diurnal, myrmecophagous, and spatially clumped, with terrestrial egg deposition and the use of phytotelmata for tadpole development. Many species have elaborate, stereotyped courtship, territoriality, and parental care (e.g., see Wells 1980, Weygoldt 1987, Summers 1990). In Madagascar, members of the endemic ranoid genus *Mantella* are known to have cutaneous lipophilic alkaloids identical to those found in the dendrobatids (Daly et al. 1984, Garraffo et al. 1993, Daly et al. 1996). Furthermore, members of *Mantella* species are also small, diurnal, myrmecophagous, and spatially clumped, and oviposit in phytotelmata (Blommers-Schlösser 1979, Glaw and Vences 1994). Little else was known of their social system or behavior until now.

When Boulenger first described *Mantella* in 1882, he placed the genus in Dendrobatidae, based largely on a shared lack of teeth (Boulenger 1882). Several other taxa are known only from South America and Madagascar (e.g. iguanians, Frost and Etheridge 1989; boas, Kluge 1991), which is biogeographically consistent with current reconstructions of Gondwana (Scotese and Golonka 1992). Since Boulenger, the hypothesis of relationship between Dendrobatidae and *Mantella* has occasionally recurred (e.g. Zimmermann 1995), but there is little phylogenetic evidence to support it (e.g. Hay et al. 1995).

Given that Dendrobatidae and *Mantella* appear to be historically distinct, but convergent in many ways, and that the dendrobatids reflect social complexity not often observed in anurans, I proceeded with an investigation of the social system, ecology, and sexual selection of *M. laevigata*. Darwin (1871) first recognized the phenomenon of sexual selection (which increases reproductive success, rather than survivorship), and the difficulties inherent in trying to assess its effects. Bateman (1948) found that, in *Drosophila*, there is higher variance in the reproductive success of males than of females. Trivers (1972) later suggested that sexual selection is delimited by the relative parental investment of each sex in offspring. In species with parental investment, the sex of the parent who invests more (usually females) is limiting for the other sex. Emlen & Oring (1977) hypothesized that the ability of a portion of a population to control access of others to potential mates determines the degree of variance in mating success. Alexander & Borgia (1979) further defined the difference in reproductive effort between the sexes: males spend more time and energy in mating effort, whereas females expend more energy in parental effort.

In light of this background theory, and bearing in mind what was known from the dendrobatids, my research revolved around questions of how much, if any, post-mating parental investment was occurring in *M. laevigata*; how both males and females assessed potential mates; and how, if at all, resources were controlled (chapters two, five and six). To investigate these questions in a species whose social system and behavior were unknown, it was imperative to broaden the scope of my research to include the population ecology of not only *M. laevigata*, but of any members of its community with which it competed or had shared interests (chapter four). Furthermore, the issue of resource control, first promoted by Emlen and Oring (1977), required an understanding of what resource, or resources, were limiting for the populations I was studying (chapter three).

Relationships Among Chapters

I wrote chapters 2-6 as independent papers to be published in journals, and as such, there is some redundancy between these chapters, such as in the description of the study site. All of the research presented was a coherent and internally coordinated enterprise. The questions I asked grew from observations in the field, from theory, and from one another, such that there is necessarily reliance on results from earlier chapters in later ones (and, to a lesser degree, vice versa).

Chapter 1 (Anuran Diversity: Reproductive Modes and Parental Care) is a review of the literature on anuran reproductive modes and parental care. This is the only chapter that does not include original research. It is included to orient the reader to the diversity of life history strategies in anurans. I focused on strategies employed by anurans, such as *Mantella laevigata*, that breed in phytotelmata (the small wells of water found within or upon plants). I proposed a new system for classifying types of anuran parental care, and reviewed fully the evidence for type 6: maternal feeding of tadpoles. At this time, several species of dendrobatids exhibit this type of parental care, as do two species of hylids, one rhacophorid, and, with this dissertation, one ranid, *M. laevigata*.

Chapter 2 (Social and Reproductive Behavior in *Mantella laevigata*, with Comparisons to the Dendrobatids) is in press in *Animal Behaviour* (manuscript #A8794). It represents the observational (non-experimental) results from this research, those 925 hours of focal observation that allowed me to put together a coherent picture of the social system and reproductive behavior of *M. laevigata*.

The questions asked and experiments undertaken in the ensuing chapters were often a result of observations reported in chapter 2.

Chapter 3 (Reproductive Limitation by Oviposition Site in a Treehole Breeding Madagascan Poison Frog (*Mantella laevigata*)) is in submission at *Evolutionary Ecology*. Based on observations during focal watches, I hypothesized that oviposition sites were limiting for this species. In this chapter I present the experiment that I conducted to test this hypothesis, and review the risks associated with breeding in phytotelmata.

Chapter 4 (*Not in My Phytotelm*: Of Neighbors, Architecture, and Water Quality: Correlates of Well Use by *Mantella laevigata*) presents a more inclusive picture of the phytotelm-dwelling community. Based on long-term monitoring of 53 individual phytotelmata, I investigated possible correlates of *M. laevigata* reproductive success such as water chemistry, water holding potential, and other inhabitants (including several other species of anurans, and insect larvae). The role of particular predators and competitors, reviewed in general terms in chapter 3, is quantified and discussed.

Chapter 5 (Female Mate Choice for Oviposition Site Quality in *Mantella laevigata*) is in submission at *Oecologia*. Based on observations during focal watches (chapter 2), and the results of limitation experiments (chapter 3), I hypothesized that females are choosing their mates based solely on their territories ("good resources"), rather than on their individual quality ("good genes"), or ability to call for long periods of time ("good current condition"). In this chapter I present the experiment I conducted to test this hypothesis, and discuss the significance of resource-based mate choice, which is common in birds but little known in anurans.

Chapter 6 (Mechanisms of Male Reproductive Success in *Mantella laevigata*) represents an investigation of those parameters that affect male reproductive success in this system with strong female choice. Using focal observations and male choice experiments to evaluate these parameters, I assessed the occurrence and relative importance of multiple male strategies, male-male competition (including prior resident advantage), male parental care, male mate choice, and male-female conflict in this species.

Ode to Amphibians

In 1758, Linneaus had this to say about amphibians:

> "These foul and loathsome animals are abhorrent because of their cold body, pale color, cartilaginous skeleton, filthy skin, fierce aspect, calculating eye, offensive smell, harsh voice, squalid habitation, and terrible venom; and so their Creator has not exerted his powers to make many of them."

After several years conducting research on said beasts, during which time I have grown quite fond of them, I would like to take this opportunity to disabuse the reader of any lingering doubts he or she may have as to the true nature of amphibians. With regard to the subject of the present volume, however, I must agree with Linneaus on two counts. *Mantella laevigata*, one of eleven currently recognized species of *Mantella*, the Madagascan poison frogs, does indeed carry with it a terrible venom, though not in such abundance as to worry the human observer, unless he intends the little frogs as a meal. And, as I hope will become evident over the course of these six chapters, *M. laevigata* must indeed have a calculating eye—and ear, and brain, for that matter—to undertake the constant assessments and reassessments necessary to exist and thrive in the complex social world it has created for itself. For that, we should not disdain the creatures, but rather, find occasion to study them further, for they are indeed captivating.

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