CONCLUSIONS

Mantella laevigata is a toxic Madagascan frog (Mantellinae: Ranidae: Anura) that is aposematically colored, small, terrestrial, diurnal, and breeds in rain-filled phytotelmata, the small pools of water found in plants. In the field, I undertook the first study of its social system and evolutionary ecology, and the ecology of members of the phytotelm guild with whom it shares oviposition sites.

The study of animal behavior relies on a solid understanding of an organism's requirements, be they for survival (naturally selected) or for reproduction (sexually selected); its ecology, and that of the organisms with whom it interacts; and basic life history characters such as diet and social system. Because Madagascar is remote, and its borders have been closed until recently, few people have asked these questions of any Malagasy animals besides lemurs. The background ecology and life history on which most behavioral studies are based does not exist for Malagasy anurans. When embarking on a study of the evolutionary ecology of a species about which little is known, one must discover the basics before proceeding to complex questions predicted by theory. This requires a combination of literature review to appreciate what is predicted by theory, and to understand the breadth of diversity already known; assessments to predict which species might reveal behaviors worth studying; long hours of observation, during which the researcher tries to discover pattern and meaning;

hypothesis generation based both on these observations and theory; experimental design and execution to assess those hypotheses; and a constant return to observation as a source of knowledge, which produces new hypotheses, and new questions, which, in turn, require answering before the system can be understood as a functioning whole. Such is the research cycle for discerning the evolutionary ecology of a species for which there is little prior background information. This dissertation reflects that process.

In this volume, I reviewed the literature on anuran reproductive modes and parental care, and proposed a new organization to describe the types of anuran parental care (Chapter 1). Phytotelm-breeding, which is most common in the wet tropics, is associated with a few highly specialized reproductive modes, and each of these is associated with a high degree of parental care. Parental care type 6, maternal feeding of trophic eggs to tadpoles, is currently known in only four anuran families, including several species of dendrobatids, two species of hylids, one rhacophorid and, with this dissertation, one ranid.

I described the social system and behavioral ecology of *Mantella laevigata* (henceforth *Mantella*), based on 925 hours of observation (Chapter 2). These comprised the basis for the hypotheses tested and questions posed in the remaining four chapters of the dissertation. Several complex behaviors were discovered, including extended male-male fights over defended resources necessary for the reproductive success of both sexes; stereotyped, highly tactile courtships in which the female may reject initial oviposition sites; and maternal feeding of tadpoles. Behavioral convergence with the Neotropical dendrobatids, which have identical skin toxins, is discussed. Clutch size is one, which was

previously unknown in anurans. Larval crane-flies (tipulids) predate eggs, and two other treehole-breeding anurans (*Plethodontohyla notostica* and *Anodonthyla boulengeri*, both microhylids) compete for space with *Mantella*.

Oviposition sites are a critical parameter of reproductive success in any species that does not move its young immediately after laying. Observations in *Mantella* suggested that they might be limiting for this species; experiments supported this hypothesis (Chapter 3). I discuss the occurrence of multiple limiting factors, and why, in this system, they have not evolved. I also considered the particular benefits of phytotelmata as breeding sites, and concomitant risks to young, including desiccation, predation, cannibalism and competition.

Phytotelmata can provide relatively safe refuges for a variety of organisms (Chapter 4). In order to understand the correlates of use and reproductive success of *Mantella* in these limiting oviposition sites, I monitored wells for several months, collecting data on water chemistry, water holding potential, and other inhabitants. *Mantella* oviposition is positively correlated with low pH; short, wet wells; and few tipulids, conspecific tadpoles, or heterospecific frogs. *P. notostica* adults protect preexisting *Mantella* eggs, but discourage new oviposition. After *Mantella* metamorphs disperse from a well, reproductive activity increases. I delineate a foodweb of the phytotelmata of NE Madagascar.

The theoretical core of this research is sexual selection (Chapters 5 and 6). In the experiment presented in Chapter 5, females were allowed to choose between calls of individual males ("good genes"), of varying length calls ("good current condition"), in different quality territories ("good resources"). My previous observations of females scouting for oviposition sites before courtships, males leaving courtships to engage in territorial defense of oviposition sites, and

biparental care, suggested the "good resources hypothesis." This hypothesis was supported, and I discuss why this system fits a model more common to birds than anurans.

Finally, I assessed mechanisms of male reproductive success in this species with strong female choice (Chapter 6). *Mantella* males affect their reproductive success through direct male-male competition, by adopting one of several mating/territorial strategies. Only males that defend limiting reproductive resources are likely to procure matings. Males adopting either of two other, less successful, strategies must be sneaky to obtain mates. In order to become and remain territorial, a male must win fights. Predictors of success in territorial encounters include prior residency, and fight initiation. Males also provide paternal care both in the form of egg attendance, and through manipulation of male-female conflict. A male can indirectly feed his young by deceiving a courted female into ovipositing into a well that already contains his tadpole.

Mantella laevigata has a complex social system that is context-dependent, in which the players are constantly assessing relevant factors and basing their behavior on these reassessments. Predators, competitors, cannibals, and desiccation all put individuals at risk, but populations thrive. Natural variation in the abiotic parameters of oviposition sites results in niche partitioning among competing species. Males and females have different interests, and their behavior is accordingly divergent as well. This research reminds us that while natural selection is generally slow, with few tools at its disposal, it remains a remarkably powerful force, capable of subtle alterations of organisms in the service of their genetic fitness.