

# REPRODUCTIVE LIMITATION BY OVIPOSITION SITE IN A TREEHOLE BREEDING MADAGASCAN POISON FROG (*MANTELLA LAEVIGATA*)

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## ABSTRACT

Oviposition sites are critical to the reproductive success of any egg-laying species, particularly those that do not transport eggs immediately after laying. I subjected *Mantella laevigata*, a Madagascan poison frog, to experimental manipulation to determine whether oviposition sites are limiting for this species. The hypothesis that oviposition sites—water-filled treeholes—are limiting for *M. laevigata* was based on my previous observations that females leave courtships to defend their oviposition sites, males leave courtships to defend their oviposition site-containing territories, and females choose mates based solely on oviposition site quality. I found that oviposition sites are limiting for *M. laevigata*. These results are discussed in light of theoretical predictions of multiple versus single limitation. Given that oviposition sites are the single limiting resource for these frogs, the advantages of being choosy about oviposition sites, and the benefits and risks of using treeholes, are delineated. Benefits include an increased ability to keep track of offspring, which may facilitate the evolution of clutch size reduction, parental care, and nest site defense. Risks primarily involve threats to young, including desiccation, predation, cannibalism and competition.

Keywords: limiting factor, reproductive success, phytotelmata, breeding site, predation, cannibalism, competition, Mantellidae

## INTRODUCTION

Limiting resources are those which, if increased, would result in an increase in population size. The limiting element for a population can act in multiple ways, but its final effect is always the same. Adding more of a limiting resource may cause existing individuals to become larger or more fecund, resulting in population growth in the next generation from increased offspring production, while the death rate remains stable. Alternately, the mechanism may be that the limiting agent causes increased immigration and reduced emigration from an area, such that population growth is a result of increased numbers in the current generation, resulting in larger future generations as well. In systems with either of these mechanisms, the limiting agent may be nutrients, water, space, shelter from weather or predators, or oviposition sites. In anurans, reproductive limitation—such as by oviposition sites—has only been demonstrated experimentally in two species (*Eleutherodactylus coqui*: Stewart & Pough, 1983; and *Dendrobates pumilio*: Donnelly, 1989).

There are three ecological positions regarding the number of limiting resources that an organism or population may experience at one time: one, several, or all resources used by that organism. The “law of the minimum” suggests that growth is limited by a single resource at any one time: a plant will grow in response to the addition of its single limiting resource, until it becomes limited by another resource (Von Liebig, 1855). In contrast, Hutchinson (1941) argued that many factors may contribute simultaneously to an organism’s success. Taking Hutchinson’s argument further, optimality theory suggests that organisms should minimize effort spent seeking non-limiting resources, and maximize time spent searching for and acquiring a limiting resource. One conclusion of optimality theory is therefore that morphology, physiology and behavior will be

altered over evolutionary time such that no resource is taken up in excess, and all resources will ultimately simultaneously limit growth of an individual or population (Chapin *et al.*, 1987; Gleeson & Tilman, 1992).

While there is little empirical evidence for organisms adjusting allocation such that all resources equally limit growth, the conditions that prescribe whether organisms will be subject to single versus multiple limitation are of considerable interest. Multiple limitation is predicted by economic models which presume that resources are not equally costly to obtain. Resources have both an absolute cost and costs relative to other resources, known as their exchange ratios (Bloom *et al.*, 1985). The extent to which a resource is limiting will depend on its exchange ratio with other resources, which depends on supply, demand, and the type of reserve being expended to acquire resource (Bloom *et al.*, 1985). Organisms that can be selected to equalize exchange ratios are predicted, as a result, to have multiple limiting factors. Examples of multiple limitation include several plant species in which multiple resources limit productivity (*e.g.* Bloom *et al.*, 1985; Campbell & Halama, 1993; Meekins & McCarthy, 2000). Additionally, in some arthropod, bird, and mammal species, multiple limitation or habitat quality mediation of limiting factors has been observed (*e.g.*, Newton *et al.*, 1994; Joern & Behmer, 1997; Schetter *et al.*, 1998).

Selection cannot also equalize exchange ratios, however, and under these circumstances single limiting resources are predicted. Changing environmental conditions make availability of resources unpredictable, which will restrict the ability of organisms to adjust the allocation of resources such that they limit growth equally. If the exchange ratio of two resources is highly skewed, the organism may experience a situation of diminishing returns, such that increases in effort

yield smaller and smaller increases in availability. At some point, it is not worth the metabolic cost to obtain a new supply of resource, either because it is too difficult to extract from the environment, or because the organism must travel too far to access it. Thus, some systems will retain a single limiting factor. In such cases, organisms are likely to exert intense effort in competition over available resources rather than in seeking new resources (see Discussion).

I studied resource limitation in *Mantella laevis*, one of approximately 17 species of Madagascan poison frog (Mantellidae). Adults of this species prey opportunistically on mites, ants, and other small terrestrial and flying insects. Males call regularly from defended territories, which include oviposition sites (water-filled phytotelmata: wells in bamboo or tree holes). Females only approach males issuing advertisement calls; after attracting a female, the male leads her to possible oviposition sites (Heying, 2001). Females assess oviposition sites both before and during courtship, and most often abandon courtships only after investigating the oviposition site that the male has led her to. Males engage in one of three territorial strategies, the most dominant and successful of which is to defend their territories against other males, who often attempt to sneak matings in oviposition sites not their own. Males often abandon courtships in order to engage in territorial defense (Heying, 2001). Females do not base mate selection on the quality or length of male calls; choice is based solely on the quality of oviposition sites in a male's territory (Heying, *in prep*). Clutch size is usually one, and females provide facultative maternal care to their tadpoles by feeding them unfertilized trophic eggs (Heying, 2001). Tadpoles obtain most of their nutrition not through maternal provisioning but by cannibalizing fertilized eggs. While mating pairs oviposit on the side of the well—above the water line and out of reach of tadpoles—fluctuating water levels and the lunging of tadpoles often bring fertilized eggs into reach, allowing tadpoles to parasitize the reproductive efforts of mating pairs (Heying, 2001).

The observations that females leave males after assessing oviposition sites, that males leave courtships to defend their oviposition site-containing territories, and that females choose mates based solely on oviposition site quality, all suggest that high-quality oviposition sites may be limiting for *Mantella laevis*. This hypothesis prompted the current research, the goal of which was to answer the following questions: Does the abundance of wells affect population density in *M. laevis*, and do wells that are filled with water attract significantly more *M. laevis* than wells that are not filled?

Organisms with multiple limiting resources are not expected to respond to experiments in which single resources are increased in the short term. The experiment described here, in which oviposition sites were added to a population of *Mantella laevis*, is therefore a test both of whether oviposition sites are limiting for *M. laevis*, and of whether oviposition sites are the *only* limiting factor for *M. laevis*, as it is impossible

to demonstrate the first, without also demonstrating the latter.

## MATERIALS AND METHODS

In each of two years (1997 and 1999), I conducted an experiment to test whether oviposition sites ("wells") were limiting for *Mantella laevis*, by adding artificial wells to plots which were monitored by visual survey before and after addition of those wells. This experimental design followed from Donnelly's (1989) work on the dart-poison frog *Dendrobates pumilio*, which also use wells (bromeliads) as discrete reproductive resources.

Research was conducted on the 510 hectare island of Nosy Mangabe, which lies at the Northern end of the Bay of Antongil, five km south of the town of Maroantsetra, Toamasina province, in northeastern Madagascar (15° 30' S, 49° 46' E). Nosy Mangabe is a "Special Reserve" in the Masoala National Park, consisting mainly of 100 – 400 year old second-growth forest.

From surveys of the island of Nosy Mangabe, six areas were found (2 in 1997, 4 in 1999) in which *Mantella laevis* were occasionally seen, very few natural treeholes were found, and there were no bamboo stands within 400 m (Fig. 1). The highest density of *M. laevis* is found in and around bamboo stands, so areas near bamboo stands were avoided to prevent

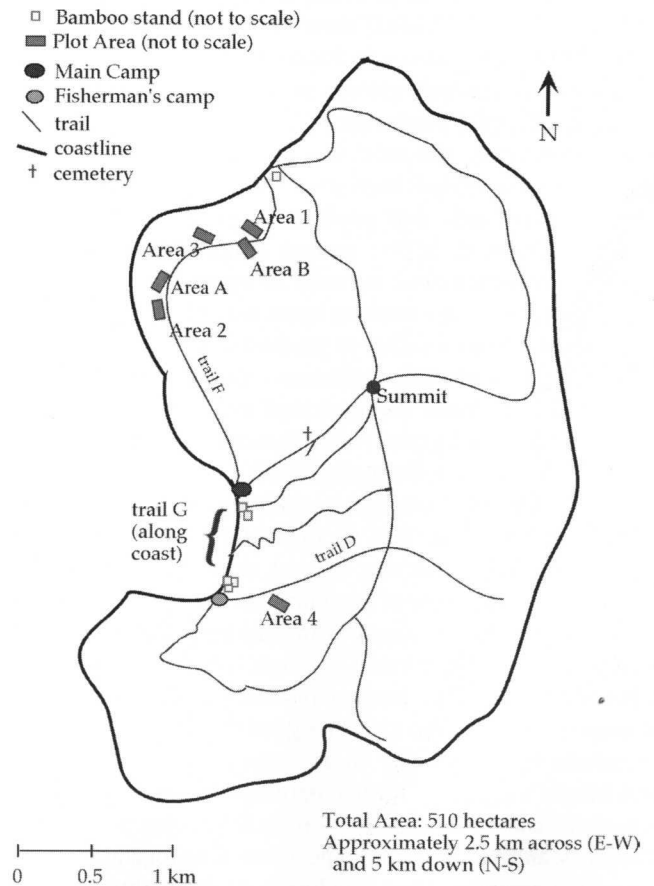


Fig. 1. Plot Areas on Nosy Mangabe.

short-term movement of individuals from known population sources. Individuals were marked by toe-clipping, waistbands, and dorsal tattoos for observation of focal populations in bamboo stands; marked individuals were never observed to move more than 100 m (Heying, unpublished data).

For each of these six unique areas, random compass directions were selected, and three plots were established, in one large transect, with the starting corner 2 meters off the nearest trail, moving in the compass direction chosen. Each transect was 10 m wide and 35 m long, and included three parallel plots which were 10 m long by 5 m wide, each 10 m apart from the next (Fig. 2).

Three days after establishing the plots, visual surveys began. Observers conducted 15 minute visual scans, with established starting points within plots, counting every *Mantella laevis* adult and juvenile observed. We surveyed the plots approximately every three days. Observers rotated through plots to control for observer effect.

After eight (1997) or six (1999) surveys, during which time each observer had surveyed each plot multiple times, one plot in each area was randomly chosen to receive artificial wells which were filled with water, and maintained ("filled well treatment"). Another plot in each area was randomly chosen to receive wells which were not filled with water, nor

maintained, except to insure that they remained upright and attached to trees ("unfilled well treatment"). The third plot in each area had no wells added to it, and served as a control plot. This design allowed for two comparisons of well use by *Mantella laevis*: 1) filled vs. unfilled vs. control plots and 2), by lumping filled and unfilled treatments into a single "well treatment," frog density in control plots could be compared with density in experimentally increased well plots.

Artificial wells consisted of small, brightly colored plastic cups, purchased in the nearby town of Maroantsetra. Seven artificial wells were placed in each treatment plot. In an effort to replicate the naturally occurring variation in well height, diameter, and volume with resources available locally, three sizes of artificial well were placed at each of three heights. Each experimental plot had identical sizes, number, and placement of artificial wells, such that comparisons between plots would be equivalent. In each treatment plot, well 1 had a 100 mm diameter, and a 575 ml capacity (filled wells were maintained at 475 ml); well 2 had a 90 mm diameter, and a 400 ml capacity (filled wells were maintained at 345 ml); and wells 3-7 had a 55 mm diameter, and a 125 ml capacity (filled wells were maintained at 95 ml). Wells 1, 3, and 5 were placed at 0.5 m above the ground; wells 2 and 4 at 1 m above the ground, and wells 6 and 7 at 1.5 m above the ground.

Three days after artificial wells were added to the treatment plots, visual surveys resumed, and continued for 14 (1997) or 18 (1999) more surveys, approximately every three days, as before. I recorded the number of adult and juvenile *Mantella laevis* seen during each survey; the observer; weather conditions; and time of day (before 1100 h, between 1100 and 1300 h, or after 1300 h).

Experimental set-up and design in 1997 and 1999 were identical, with the following exceptions. In 1997 there were only two experimental areas, in 1999 there were four. In 1997, there were two observers (the author and Jessica Metcalf), in 1999, there were three (the author, Bret Weinstein, and Glenn Fox). In 1997, eight surveys were conducted, over the course of 23 days, before wells were added to treatment plots. Fourteen more surveys were conducted following well addition, over a span of 38 days. In 1999, six surveys were conducted, over the course of 16 days, before wells were added to treatment plots. Sixteen more surveys were conducted following well addition, over a span of 46 days. The experiment was conducted during the rainy season (February through April) in both years.

This experiment was designed to maximally control for as many parameters as possible, while simultaneously allowing for several relevant statistical analyses. Statistics reported in this paper are standard non-parametric tests (Kruskal-Wallis & Mann-Whitney U, analyzed using StatView 5.0.1). Neither of these tests assume that statistically comparable groups have an equal number of data points; thus, differences in number of plots and surveys between years and before and after wells were added to control plots are not problematic for these analyses. In addition, this experimental design controlled for

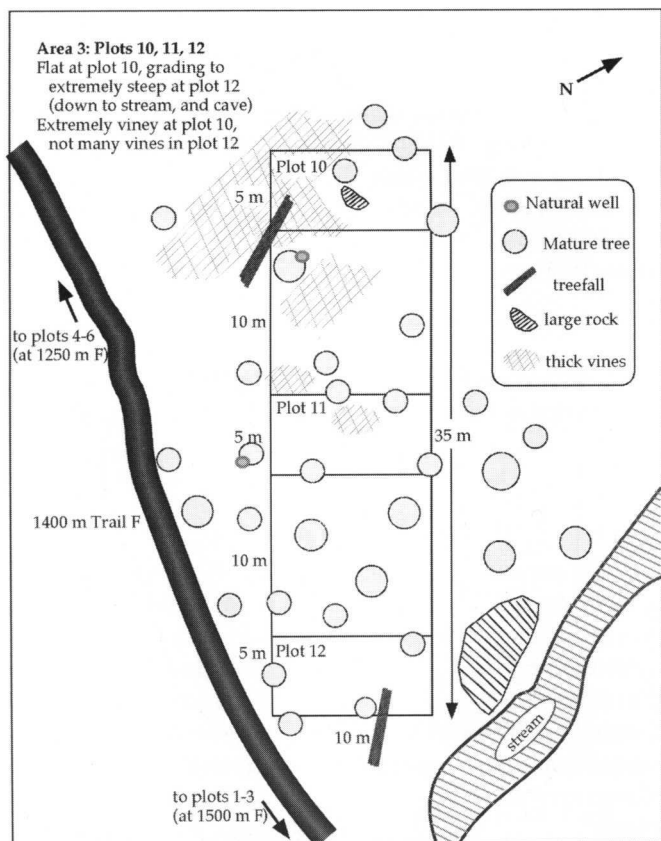


Fig. 2. Physical Environment of Area 3, with parallel plots.

parameters such as effects due to observer, weather, time of day, and differences between years. Differences in frog density between areas was expected, and as all areas were represented in all analyses, merely constitutes noise in the data.

## RESULTS

The presence of artificial wells is correlated with an increase in population density in *Mantella laevis*. The experimental design allows two distinct analyses of these data, both of which find significant differences between plots with wells added to them, and plots without wells added. The first analysis compares population densities on the same plot types (control, unfilled, and filled), before and after wells were added to the treatment plots (see Figure 3). The addition of wells significantly affected population density in *M. laevis* both in plots to which unfilled wells were added (Mann-Whitney U,  $U = 1258.0$ , tied- $p = 0.002$ ), and in plots to which filled wells were added (Mann-Whitney U,  $U = 1473.0$ , tied- $p = 0.040$ ). By contrast, control plots, to which wells were never added, did not differ significantly between the same time periods, although there was an unexpected, non-significant trend for frogs to leave these plots, probably as a result of movement into neighboring treatment plots (Mann-Whitney U,  $U = 1764.0$ ,  $p = 0.406$ , Fig. 3).

The second analysis compares population densities in control (plots to which no wells were ever added) versus treatment (all plots to which wells were added—filled plus unfilled) plots, after wells were added to the treatment plots (see Fig. 4). When treatments are lumped this way, and treatment plots are compared to control plots for surveys 7–24 only (after wells were added), all plots with wells in them attracted significantly more *Mantella laevis* than did control plots (Mann-Whitney U,  $U = 5121.5$ ,  $p < 0.0001$ , Fig. 4).

Contrary to expectation, unfilled-well plots attracted significantly more frogs than did filled-well plots (Mann-Whitney U,  $U = 4311.0$ ,  $p = 0.008$ ), although unfilled-well plots had a non-significantly higher baseline as well (Mann-Whitney U,  $U = 606.0$ ,  $p = 0.594$ , Fig. 5). Due to chance, baseline population densities of control plots were non-

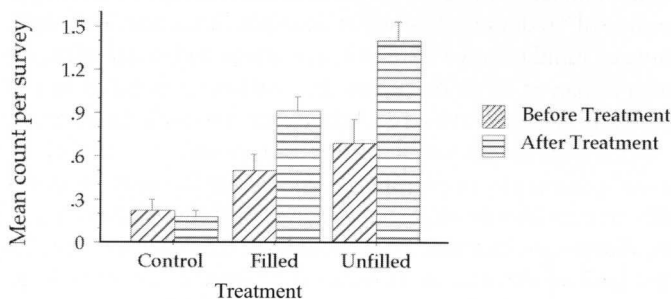


Fig. 3. Population density of *Mantella laevis* increases with the addition of wells to experimental plots. Population density increased significantly in "unfilled" plots after the addition of wells, but not in "filled" or "control" plots. Data reported are Means  $\pm$  S.E. See text for statistical details.

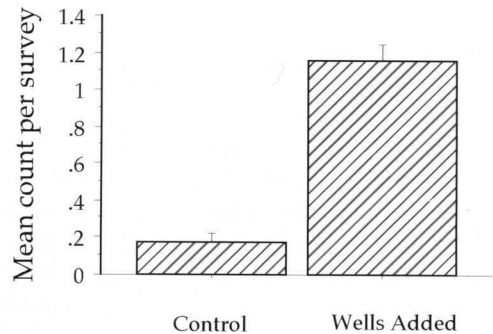


Fig. 4. Population density of *Mantella laevis* is higher in plots with wells added than in control plots. During concurrent surveys, plots with wells added to them attracted significantly more *M. laevis* than did control plots. Data reported are Means  $\pm$  S.E. See text for statistical details.

significantly lower than those of either unfilled-well or filled-well plots.

The six distinct areas, in each of which three plots were laid (2 in 1997, 4 in 1999), were significantly different from each other with respect to frog density (Kruskal-Wallis,  $H = 27.112$ ,  $p < 0.0001$ , Fig. 6). Weather also affected the numbers of frogs counted, with cooler, wetter weather generally being correlated with higher numbers of observed frogs (Kruskal-Wallis,  $H = 11.145$ ,  $p = 0.0079$ , Fig. 7). This result is even more clear when the weather data is collapsed into two categories: hot and/or dry, and wet and/or cool (Mann-Whitney U,  $U = 18608.0$ ,  $p < 0.0021$ ). Time of day had no significant effect on observed population density (Kruskal-Wallis,  $H = 2.562$ ,  $p = 0.2039$ , Fig. 8), nor did observer (Kruskal-Wallis,  $H = 2.985$ ,  $p = 0.2952$ ). Year did have a significant effect on population density of *Mantella laevis*, with significantly more individuals observed per survey in 1997 than in 1999 (Mann-Whitney U,  $U = 15893.5$ ,  $p = 0.0027$ ).

## DISCUSSION

Wells are limiting for *Mantella laevis*. As only two previous studies have experimentally demonstrated population

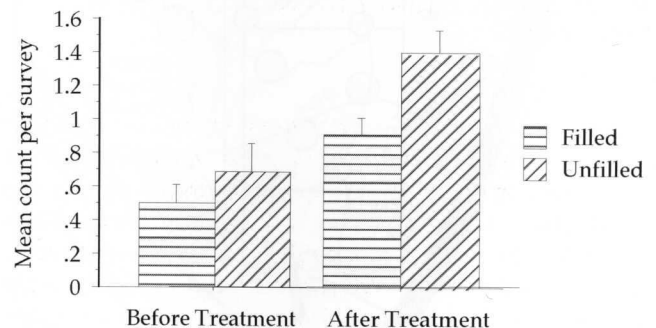


Fig. 5. Effect of unfilled versus filled wells on population density of *Mantella laevis*. Plots containing unfilled wells attracted significantly more frogs than did plots containing filled wells. Data reported are Means  $\pm$  S.E. See text for statistical details.

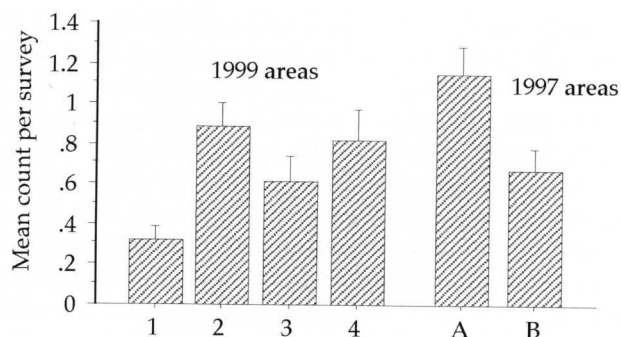


Fig. 6. Area Has an Effect on Population Density of *Mantella laevis*. Data reported are Means  $\pm$  S.E. See text for statistical details.

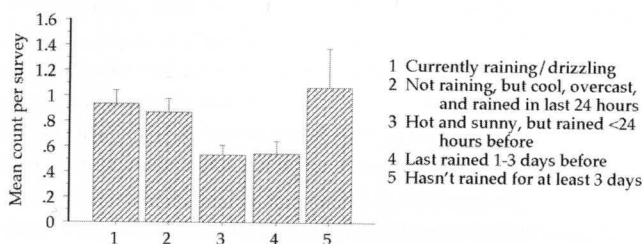


Fig. 7. Weather has an effect on observed population density of *Mantella laevis*. Data reported are Means  $\pm$  S.E. See text for statistical details.

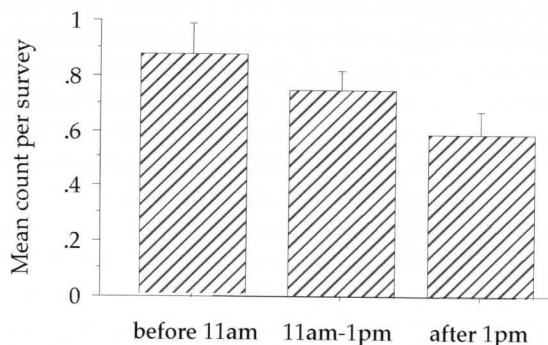


Fig. 8. No time of day effect on observed population density of *Mantella laevis*. Data reported are Means  $\pm$  S.E. See text for statistical details.

limitation by reproductive resources in anurans (Stewart & Pough, 1983; Donnelly, 1989), this work provides an important example of what is likely to be a larger trend. My two experimental treatments (unfilled-wells added versus filled-wells added) did not differ, probably because, during the rainy season, unfilled wells quickly fill and remain filled naturally with rainwater. Having a well that is maintained at a constant level and cleaned of excess detritus is an evolutionary novelty, and one that *M. laevis* should not be expected to respond to if it provides no benefit. Indeed, the addition of rainwater and regular disturbance by humans might be a deterrent, making

the filled wells less desirable than the unfilled ones in times of water excess, although all wells, of both treatment types, were visited and manually disturbed after each survey to control for experimenter influence. During a time of drought, when the unfilled wells were in fact empty of water some of the time, I would predict a difference between these two treatments. During the dry season this might also be true, although much lower rates of breeding during the dry season would make it difficult to collect enough data to test this prediction (Heying, *personal observation*).

Other changes in population density found during this study include that the "control" plots showed a trend towards decreases in population density after the wells were added in the treatment plots. This is likely due to emigration out of those plots, which suggests that the mechanism of limitation in this system is to reduce immigration when resources (wells) are in short supply. Due to the relatively short time period of the study in each year, it is unlikely that observed population density increases were due to an increase in birth rates, although future studies might benefit from describing the age structure of the population before and during the experiment. The populations affected by this study are spatially restricted enough that a local bounty—such as the addition of 14 artificial wells within a single area—apparently causes emigration from the one plot without additional wells.

I failed to falsify my hypothesis that wells are limiting for *Mantella laevis*. This begs the question, in light of earlier arguments regarding multiple limiting resources: What about this system has caused natural selection to allow a single limiting factor?

Multiple limitation occurs when effort devoted to acquiring a non-limited resource is shunted towards effort to acquire a limited resource. When extra, limited resource can be obtained by exchanging effort in this way, natural selection will tend to equalize availability of multiple resources. For instance, if there were an infinite number of oviposition sites (wells) in the environment of *Mantella laevis*, the frogs would need only find those wells in order to utilize them. By converting the non-limiting resource of food into the energy used to discover additional (limiting) wells, the frogs could, theoretically, ultimately exist in a system of multiple limitation. But wells are not infinite, and all wells in the unmanipulated system are already being used. No matter how much food energy is put into searching for new oviposition sites, there will be no more; other resources cannot be converted into wells.

*Why breed in treeholes?* Anuran treehole (well) breeders utilize a distinct niche during their larval stage. In the absence of direct development or extreme behavioral adjustment on the part of the parents (found in the gastric brooding frog, or when one of the parents carries the clutch on its back), which is known from very few anurans, these species must go through both an egg and tadpole stage in which they rely on a single environment. The larval environment is the result of oviposition site choice by one or both parents.

*Mantella laevisgata* occurs on Nosy Mangabe and the Masoala peninsula, in neither of which do small ponds of surface water exist. The fresh water in these forests is found in rivers; small, fast moving streams that flood regularly during the rainy season; and treeholes. In a species that currently uses treeholes, the adaptive valley between this state and the nearest possible one, that of using small, fast moving, often-flooded streams, is vast and deep. Moving between these two adaptive peaks would require a set of modifications in the offspring that would be distinctly suboptimal in these two, divergent habitats (Wright, 1932).

*Mantella laevisgata* has a clutch size of one, which is apparently adaptive in a treehole breeding environment in which parents can keep track of their offspring (Heying, 2001). However, this minimal clutch size would almost certainly condemn a high proportion of eggs laid to either physical mutilation in the fast moving environment of a stream or river, or to predation, especially by fish or dragonfly larvae, known predators of amphibian eggs and larvae in other systems (e.g., Resetarits & Wilbur, 1989; Kats & Sih, 1992; Hopey & Petranka, 1994; Holomuzki, 1995).

Minimal clutch size is possible in *Mantella laevisgata*, in part, because of the reduced number of predators in treeholes. Release from predation is a clear advantage to breeding in restricted water bodies. Furthermore, treeholes provide an easily defensible territory for males, which allows them to increase their certainty of paternity by excluding other males. Continuing defense of and courtship in wells already containing tadpoles constitutes, at the very least, passive paternal investment by the male territory holder. Males dissuade other anuran species that breed in treeholes from displacing tadpoles. And eggs resulting from later courtships between the father/territory holder and an unrelated female often go to feed an existing tadpole (Heying 2001). Females gain whenever males invest in offspring. Defense of retreat sites offers advantages to both sexes in *M. laevisgata*, which is similar to the system described for *Eleutherodactylus coqui* in Puerto Rico (Stewart and Rand, 1991).

*Why be choosy about oviposition site quality?* Resetarits (1996) argues that oviposition site choice must be under equally strong selection as egg and clutch size in order to generate locally adapted life history phenotypes and optimize parental fitness. If oviposition site quality is variable, and correlated with offspring success, both sexes are expected to be selective. In *Mantella laevisgata*, females are choosing oviposition site and *not* male quality or current condition (Heying, *in prep*), suggesting a particularly important role for oviposition site quality in reproductive success in this species.

Oviposition sites act as patches, each of which contain both resources and risk (Resetarits, 1996). In the Masoala, the resources available to *Mantella laevisgata* in high-quality treeholes include territorial defense by the resident male against intruding competitors; and deep and therefore reliable water, which is likely to attract future courtships, thus providing food

for tadpoles in the form of fertilized eggs (Heying, 2001). The risks of low-quality treeholes include desiccation, predation, cannibalism, and competition from heterospecifics.

Desiccation of eggs or larvae is a risk for amphibians. Semlitsch and Gibbons (1990) found that pond drying is inversely correlated with larval success in salamanders. In treehole breeders, the amount of water in the well and the humidity are both known to affect survivorship (damselflies – Fincke, 1994; rhacophorid frogs – Kam *et al.*, 1998). Several studies have revealed a preference for moist or wet oviposition sites in amphibians (treefrogs – Crump, 1991; salamanders – Figiel & Semlitsch, 1995; ranid frogs – Spieler & Linsenmair, 1997). *Mantella laevisgata* do not oviposit in dry or shallow wells (Heying, *in prep*).

Predation is reduced in treeholes, but is a prominent source of mortality for most anuran eggs and tadpoles. In several species, adult anurans choose oviposition sites that reduce the risk of predation, and there is evidence from Amazonian frogs that treehole breeding may have evolved as a response to predation pressure from aquatic predators such as tadpoles and beetle larvae (Magnusson & Hero, 1991). Documented pairs of anuran prey with their avoided predators include bullfrogs and leeches (Howard, 1978); treefrogs and both salamanders and fish (Resetarits & Wilbur, 1989); wood frogs and fish (Hopey & Petranka, 1994); squirrel treefrogs and banded sunfish (Binckley & Resetarits, 2002); American toad larvae predated by wood frog tadpoles (Petranka *et al.*, 1994); pickerel frogs and American toads predated by fish (Holomuzki, 1995); and red-eyed tree frogs predated by shrimp (Warkentin, 1999). In treeholes, the risk of predation from salamanders, fish and shrimp is essentially zero, but larval insects can co-occur with tadpoles in treeholes. In Brazil nut fruit capsules, which are analogous to treeholes by virtue of acting as restricted, temporary oviposition sites, poison frog tadpoles are susceptible to predation by both mosquito and damselfly larvae (Caldwell, 1993). In bamboo wells, chironomid and tipulid larvae prey on the eggs of well-breeding rhacophorids (Kam *et al.*, 1998). And crane-fly larvae (*Limonia renaudi* Alexander, Tipulidae) prey on the eggs of at least three anuran well-breeders in the Masoala, including *Mantella laevisgata* (Heying, *personal observation*). Adult female *M. laevisgata* reject oviposition sites that contain predatory crane-fly larvae (Heying, 2001).

Cannibalism is also a threat to anuran larvae, and is therefore a parameter that females choosing oviposition sites should take into account. Crump (1991) demonstrated experimentally that female treefrogs prefer to oviposit in artificial pools lacking conspecific tadpoles, which are known to be cannibalistic. Similarly, African ranid frogs avoid ovipositing in pools where there are cannibalistic conspecifics (Spieler & Linsenmair, 1997), as do some dendrobatids (Summers, 1999) and leptodactylids (Halloy & Fiaño, 2000). In *Mantella laevisgata*, females reject oviposition sites that already contain conspecific tadpoles, though they do not reject sites with conspecific eggs (Heying, 2001).

Competition from other species is well studied in anuran larvae (see Alford, 1999 for review), but evidence of oviposition site choice based on risk of competition is less well documented. In other taxa, male gobies experience competition for nest sites from invertebrates and larger fish (Breitburg, 1987; Kroon *et al.*, 2000), and female salmon compete with related species for breeding space (Essington *et al.*, 2000). Damselflies compete for treeholes with other species of odonates (Fincke, 1992). Adults of one species of treefrog avoid ovipositing in ponds that already contain the competitive larvae of another treefrog (Resetarits & Wilbur, 1989). And in *Mantella laevis*, it is the males, rather than the females, that discriminate against oviposition sites containing competing species of microhylid frogs and their clutches (Heying, 2001).

Given the risk from desiccation, predation, cannibalism, and competition for anuran larvae generally, oviposition site choice must be critical to reproductive success. In other taxa, oviposition site preference by females has been correlated with increased parental reproductive success. Choosy damselflies show increased offspring survivorship (Siva-Jothy *et al.*, 1995), and choosy pied flycatchers gain an increase in clutch size (Siikamäki, 1995). In *Mantella laevis*, where oviposition sites are limiting, and both sexes discriminate among these oviposition sites, it is likely that parental reproductive success is enhanced by this parental behavior.

For the same reasons that many resources or factors may be simultaneously limiting, females may select multiple aspects of males/resources when choosing mates. That which is most variable in the population at the time of choice is likely to be that which is most actively chosen by females (as in sparrows, Reid & Weatherhead, 1990). If natural selection is continually readjusting the need for and availability of limiting factors, then we should expect populations to evolve in response to those changes as well. Females will choose mates differently if food is limiting and males control access to the food, than if food is widely available, and males control no resources that females require. Thus, it is important to conduct choice experiments at the same time (during the same season) as limitation experiments, in order to attempt to "match up" what is limiting with what females are choosing.

*Conclusions.* In any population, some parameter or parameters are limiting population growth. Given the propensity for natural selection to act on parameters that limit survivorship, growth, and reproduction, individuals are expected to be limited by multiple factors under most conditions. In some systems, however, multiple limitation does not occur. *Mantella laevis* is an example of one such system. The single limiting factor for *M. laevis* is treehole oviposition sites, a resource so unique in the environment of *M. laevis* that abandoning treeholes as oviposition sites would result in reproductive failure. Given the current reliance on treeholes for reproduction, *M. laevis* is expected to shunt effort spent acquiring other resources to finding and/or acquiring oviposition sites. Given a finite number of oviposition

sites, however, additional effort acquired through food energy will, ultimately, fail to result in the discovery of additional oviposition sites. If there is still excess food in the environment, which is likely for the opportunistically foraging *M. laevis*, natural selection might convert those resources into increased competition for oviposition sites. Although competition for oviposition sites is not a resource, per se, but a behavior that can lead to the acquisition of limiting resources, this prediction points to a possible role for non-limiting factors. Non-limiting food could, with increased uptake, result in increased levels of competition for oviposition sites, altering the nature of territorial disputes and, ultimately, the social system.

#### ACKNOWLEDGMENTS

I am indebted to Jessica Metcalf, Bret Weinstein, Glenn Fox, and Rosalie Razafindrasoa for field assistance. I am also grateful to Bret Weinstein for additional intellectual support and technical assistance, and to Arnold Kluge and Barbara Smuts for comments on earlier drafts of this paper. This work would not have been possible without the support of the government of Madagascar; logistical support was given by WCS, Projet Masoala, and MICET. This research was supported by grants from Animal Behaviour, Sigma Xi, the University of Michigan Museum of Zoology, the Department of Biology, and the Horace H. Rackham Graduate School, and the Sokol International Research Fellowship.

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