

# Competitive interactions and distributional dynamics in two Malagasy frogs

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**Abstract:** Ecological theory predicts that interspecific interactions can affect population and community dynamics. Two experiments were conducted on *Mantidactylus bicalcaratus* and *M. punctatus*, two sympatric frog species from Madagascar that live and breed in rain-forest plants (*Pandanus* spp.), to test for interspecific competition. The first experiment examined larval growth rates and survivorship with and without conspecifics. While survivorship did not differ among treatments, mean growth rates for *M. bicalcaratus* were significantly reduced in the presence of *M. punctatus* larvae. The second experiment manipulated the presence and density of adults in *Pandanus* plants. Emigration from and immigration to experimental plants tended to be higher and lower, respectively, for *M. bicalcaratus* in the presence of *M. punctatus*, but these differences were not significant. These results demonstrate asymmetric competition (at least as larvae) and indicate that *M. punctatus* is the superior competitor. Field data showed that *M. bicalcaratus* was found significantly more frequently in the absence of *M. punctatus*. Also, *M. bicalcaratus* populations were significantly more likely to go locally extinct in the presence of *M. punctatus*. These data suggest that asymmetric competitive interactions are important influences on the dynamics of these populations.

**Key Words:** Amphibia, coexistence, Madagascar, *Mantidactylus*, *Pandanus*, phytotelmata, population dynamics, tadpoles

## INTRODUCTION

A large amount of experimental evidence indicates that interspecific competition can have an important influence on individual fitness, population dynamics and community composition (reviews in Connell 1983, Schoener 1983). In particular, interspecific competition has often been suggested as an important factor determining distribution patterns. In a now classic study, Hairston (1980) demonstrated the effect of interspecific competition on species distributions by manipulating populations of two sympatric salamanders. Unfortunately, while competition experiments have frequently been conducted, the results have only rarely been related back to field distributions.

Amphibian larvae have been used often in such experiments because of the relative ease with which these aquatic organisms are manipulated, and data from a relatively large number of laboratory, mesocosm and

field studies are available (see reviews in Alford 1999, Morin & Johnson 1988). In contrast, experimental investigations of competitive interactions in adult amphibians have rarely been conducted, even though competition among adults may have far-reaching consequences. Even more uncommon are studies of organisms with complex life cycles in which interspecific competitive interactions in both larvae and adults are assessed. Although a few pioneering tropical studies are available (e.g. Inger & Greenberg 1966) the vast majority of work on interspecific competition in amphibians has been conducted in North America or Europe, and few data are available on the competitive interactions of tropical species.

Because of close phylogenetic relationships, sister species will share many characteristics and are expected to have greater niche overlap than phylogenetically distant species. If interspecific competition between sister species is intense enough, it is thought that either natural selection will favour the evolution of niche differentiation or competitive exclusion will occur (Tokeshi 1999). As a result, many investigators have looked for evidence for interspecific competition among closely related species

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**Table 1.** Mean growth rates ( $\text{mm d}^{-1}$ ) of *Mantidactylus bicalcaratus* and *M. punctatus* larvae in experimental microcosms. Each treatment was replicated three times. Superscripts indicate sets of means that are significantly different using a one-way ANOVA with Bonferroni post-hoc tests.

Treatment									
<i>M. bicalcaratus</i> per container	4	8	12	8	4	4	–	–	–
<i>M. punctatus</i> per container	–	–	–	4	4	8	12	8	4
Growth ( $\text{mm d}^{-1}$ )									
<i>M. bicalcaratus</i>	0.729 <sup>a</sup>	0.68 <sup>a</sup>	0.421 <sup>b</sup>	0.342 <sup>c</sup>	0.452 <sup>b</sup>	0.32 <sup>c</sup>	–	–	–
<i>M. punctatus</i>	–	–	–	0.317 <sup>a</sup>	0.443 <sup>b</sup>	0.335 <sup>a</sup>	0.309 <sup>a</sup>	0.399 <sup>b</sup>	0.542 <sup>c</sup>

(but see Blaustein & Margalit 1994, Brown & Davidson 1977). To provide information on the strength of competitive interactions between two closely related species of tropical frogs, I conducted experiments with larvae and adults of two sympatric leaf axil-breeding frogs from Madagascar. This information was then used to help explain observed patterns of distribution and dynamics in the field.

## STUDY SYSTEM

The study site is located in a remnant coastal rain forest near the village of Sainte Luce (Manafiafy), in south-eastern Madagascar ( $24^{\circ}46'S$ ;  $47^{\circ}10'E$ ). At the Sainte Luce forest, two endemic frogs (*Mantidactylus bicalcaratus* (Boettger) and *M. punctatus* (Blommers-Schlösser) are obligate inhabitants of *Pandanus* plants (screw pines). A single undescribed species of *Pandanus* (section *Dauphinensis* – M. Callmander, personal communication) is the only plant where eggs, larvae or adult frogs have been found at Sainte Luce. These *Pandanus* plants gather rainwater in leaf axils, and tadpoles of both species develop in these tiny waterbodies ( $\sim 150$  ml). Eggs are deposited on *Pandanus* leaves where they develop for up to 10 d before the hatchlings wriggle down (or are washed by rainwater) into the leaf axil below. Larvae of both species feed on detritus and development takes 2–3 mo (Lehtinen 2002, 2004). After metamorphosis, juveniles and adults remain on *Pandanus* and are exclusively found on these plants. Other research has demonstrated that these frog populations are spatially structured and have many characteristics of a metapopulation (Lehtinen 2003a). These frogs are restricted to rainforest but are widely distributed in eastern Madagascar (Glaw & Vences 1994).

The distributions of both species overlap in the field, often occurring together in the same plant or even in the same leaf axil (Lehtinen 2003a). A cladistic analysis of mitochondrial DNA sequences indicated that *M. bicalcaratus* and *M. punctatus* are sister taxa (Lehtinen *et al.* 2004). Since these two species are closely related sympatric habitat specialists and high quality *Pandanus* leaf axils are limited (Lehtinen 2003a), I expected that the probability of past or current competition was high.

## METHODS

### Interspecific competition in tadpoles

Experiments in artificial microcosms were conducted to test for interspecific competitive interactions between tadpoles of *M. bicalcaratus* and *M. punctatus*. This was done in an additive design at three density levels with and without heterospecifics such that the intensity of interspecific and intraspecific competition could be distinguished (Table 1). Each treatment was replicated three times, and the response variables were net growth rate ( $\text{mm d}^{-1}$ ) and survivorship over the course of the experiment. To show an asymmetric interspecific competitive effect, growth rates or survivorship would have to be significantly lower in the presence of heterospecifics compared with an equal number of conspecifics.

Egg masses of *Mantidactylus bicalcaratus* and *M. punctatus* were collected from *Pandanus* leaves at Sainte Luce between 25 and 29 January 2002 and reared under identical conditions until the initiation of the experiment. Egg masses were identified by the presence of attending adults (see Lehtinen 2003b). All experiments were conducted in plastic water bottles with the tops cut off (1.5 litre volume,  $200 \text{ mm} \times 90 \text{ mm}$ ). Each bottle contained 250 ml of water (50 ml from leaf axil where egg mass was taken, 200 ml rainwater), 5 g of coarse and fine detritus (dry weight, collected from a single location on the forest floor near the field laboratory), and one fresh *Pandanus* leaf (changed as necessary). Water levels were maintained at a constant level in each bottle by periodically adding rainwater. Any insect larvae present initially were removed and the tops of the containers were covered with mosquito netting to prevent subsequent insect oviposition. Larvae were randomly assigned to treatments with the constraint that all larvae in each bottle were from the same egg mass (i.e. full siblings). All treatments began with stage 22 larvae (Gosner 1960),  $7.0 \pm 1.3$  mm in total length. Similarly sized individuals were used in all treatments, since differences in size are known to affect the outcome of competitive interactions (Werner 1994). The densities in this experiment (4, 8 and 12 larvae per container, respectively) were within the range of densities found in

the field for each species. All bottles were kept out of direct sunlight and placed in random positions on a tabletop in an open-air field laboratory. Total length of all larvae in experiments was measured to the nearest 0.5 mm with calipers at the beginning of the experiment and at 10 and 22 d. Abiotic conditions in the plastic bottle microcosms were comparable to the aquatic environment in *Pandanus* leaf axils in the field (see Lehtinen 2004 for details).

### Interspecific competition in adults

I tested for evidence of interspecific competition between adults of *M. bicalcaratus* and *M. punctatus*. This was done using a whole patch addition experiment, where *Pandanus* plants in the field were emptied of their inhabitants and re-stocked at particular densities and combinations of con- and heterospecifics. Here, the response variables were the proportion emigrating and the number of immigrants to each patch. To show an asymmetric interspecific competitive effect, one species would have to be shown to emigrate more in the presence of heterospecifics than at a similar density of conspecifics. Also, if one species had significantly lower immigration in the presence of heterospecifics when compared with an identical number of conspecifics (a priority effect), this would also be consistent with a hypothesis of asymmetric interspecific competition. Inter-plant dispersal rates in unmanipulated *Pandanus* averaged 13.9% in *M. bicalcaratus* and 6.7% in *M. punctatus* over a 6-wk period with most dispersal distances being less than 15 m (unpubl. data). These data suggested that inter-plant movement rates would be moderate enough to detect differences among treatments.

Twenty-one *Pandanus* plants were selected for inclusion in the addition experiment based on the following criteria: (1) plant width was greater than or equal to 2.5 m, (2) plant height was less than 1.0 m, (3) canopy cover over the plant was between 25 and 75%, (4) the amount of water in leaf axils was 2 or greater (on 0–4 qualitative scale where zero was dry leaf axils and four was completely full), (5) the amount of detritus in leaf axils was 3 or less (on 0–4 qualitative scale where zero was no detritus present and four was completely full of organic material), (6) the distance to the nearest other patch included in the experiment was > 25 m and (7) the plant was located outside the monitoring area (see below). In addition, all patches included in the experiment had initial populations of at least two adult individuals of *M. bicalcaratus* or *M. punctatus*. Most of these criteria are related to habitat quality and were used to minimize the likelihood that transplanted individuals would leave because habitat quality differences. Since very few of the hundreds of plants examined met all of these criteria, I

**Table 2.** Characteristics of patches (n = 21) at beginning of whole-patch addition experiment. Water and detritus were measured on a qualitative scale from 0–4 (see text for details); patch quality is a composite index combining the water, detritus and canopy cover variables.

Variable	Mean ± SD or median	Range
Patch size (m)	3.3 ± 0.5	2.5–4.2
Patch height (m)	0.3 ± 0.1	0.2–0.7
Water	3.0	2–4
Detritus	2.25	0.5–3.0
Canopy cover (%)	25	25–75
Overall patch quality	10.4 ± 1.6	8–13
<i>M. bicalcaratus</i> adults	3.1 ± 2.3	0–8
<i>M. punctatus</i> adults	3.3 ± 4.0	0–16
Total adult frogs ( <i>bicalcaratus</i> + <i>punctatus</i> )	6.4 ± 4.1	2–18
Mean distance to five nearest neighbours (m)	10.5 ± 4.6	4.6–24.2

**Table 3.** Mean proportion of transplanted adults emigrating and the mean number of immigrants per treatment in the whole patch addition experiment for each species. Each treatment was replicated three times. ANOVAs were not significant for either species ( $P > 0.05$ ).

Treatment	1	2	3	4	5	6	7
<i>M. bicalcaratus</i> density	4	8	8	4	4	–	–
<i>M. punctatus</i> density	–	–	4	4	8	8	4
Mean proportion emigrating							
<i>M. bicalcaratus</i>	0.67	0.71	0.63	0.83	0.92	–	–
<i>M. punctatus</i>	–	–	0.33	0.75	0.54	0.50	0.63
Mean number of immigrants							
<i>M. bicalcaratus</i>	1.0	2.3	0.0	0.7	1.0	0.3	0.7
<i>M. punctatus</i>	3.0	2.7	2.7	1.3	2.3	3.0	1.3

used the first 21 suitable *Pandanus* plants I found, rather than randomly selecting replicates from a larger pool (see Table 2 for characteristics of the *Pandanus* plants included in the experiment). All experimental plants were randomly assigned to a treatment. Seven treatments were initiated in an additive design, each containing one species at low (four adult frogs) or high (eight adult frogs) density with or without the other species (Table 3). Each treatment was replicated three times.

From 31 January to 2 February 2002, the original inhabitants were removed from all plants used in the experiment (see Table 2 for initial conditions). Two or three visits in a 12-h period were necessary to ensure that all individuals were removed. After removal, individuals were held in plastic containers, and then randomized and re-established in a different experimental patch at 1:1 sex ratios in the treatment combinations and densities indicated in Table 3. Since only eight or nine patches could be defaunated and re-established in a day, and to minimize stress in individuals removed from their home area, frogs were placed among the experimental patches defaunated that day. Some additional adults were obtained from non-experimental patches to achieve the target densities in each treatment. Populations were established at densities comparable to both the pre-existing conditions and to those found in similar unmanipulated *Pandanus* plants (unpubl. data). All

individuals received a unique mark with toe-pad clipping, which allowed recognition of immigrants and emigrants (Donnelly *et al.* 1994). Since competitive interactions may differ between juveniles and adults, only adults were used in this experiment (defined as those individuals with a snout-vent length > 18 mm). This is the size at which secondary sexual characteristics appear (unpubl. data).

After re-establishment of frog populations in the treatment combinations, patches were left alone for 10 d. Following this period, each experimental patch was again exhaustively defaunated. Numbers of immigrants to and emigrants from each patch were quantified based on the presence or absence of the marked individuals initially established. Both species have a short life span (< 6 mo on average, unpubl. data), thus 10 d is a substantial portion of their life cycle. An addition experiment was used rather than a removal experiment to provide more control over initial conditions (especially presence-absence and density, which varied greatly in the field).

### Field distributions

The distribution of *Mantidactylus bicalcaratus* and *M. punctatus* at Sainte Luce was assessed in three networks of 15 contiguous 25 × 25-m (625 m<sup>2</sup>) plots. Each network was located at least 500 m from the nearest other network of plots (45 plots total). All *Pandanus* plants found within each plot were mapped using a compass and tape and several environmental variables were recorded for each plant (see Lehtinen 2003a for details). Each individual plant (n = 839) was surveyed for frogs during daylight hours three times in the rainy seasons of 2000, 2001 and 2002 (9 surveys total). Surveys involved visually examining all leaves and leaf axils in each plant for frogs. I searched as long as was necessary to be certain that no frogs were missed (usually less than 10 min per plant). These small frogs (*M. bicalcaratus* maximum 28 mm SVL, *M. punctatus* maximum 25 mm SVL) are conspicuously coloured, primarily diurnal and often active on the leaves of the plant. This, combined with the fact that the plants are relatively small and afforded few places to hide, resulted in high detection probabilities. I noted the presence or absence of each species, as well as the number of individuals in each age class (metamorphs, juveniles, adults) and the presence of egg masses and larvae. For the purposes of this analysis, I present only presence-absence and extinction-colonization data.

### Statistical analysis

In the larval competition experiment, I tested for significant differences in growth rates and survivorship

among treatments using one-way analysis of variance (ANOVA) using growth rate (mm d<sup>-1</sup>) and proportion of larvae surviving to the end of the experiment (arcsine transformed) as factors. I used Bonferroni post-hoc tests to make comparisons when ANOVAs were significant. I also conducted a two-way ANOVA to determine if *M. bicalcaratus* and *M. punctatus* had different growth rates in the presence of heterospecifics. These data were obtained by subtracting the mean growth rate at a given density of heterospecifics from the mean growth rate at the same density of conspecifics. Therefore, if growth was reduced in the presence of conspecifics (relative to the same density of conspecifics), this calculation produced a negative number. Container means were used in all analyses.

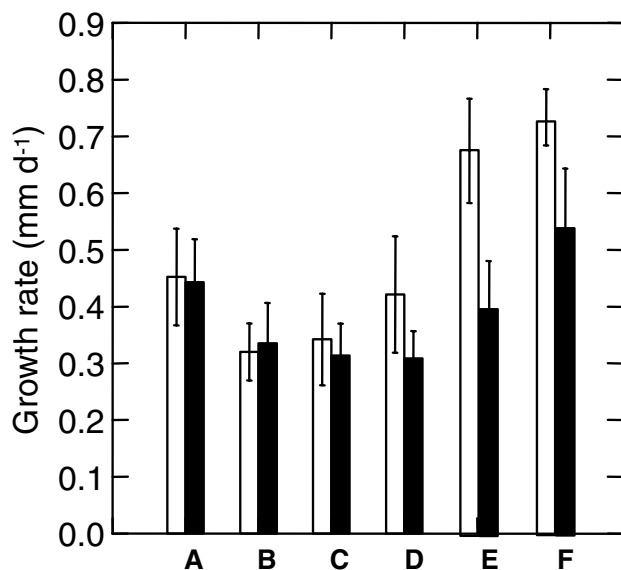
In the adult addition experiment, I tested for significant differences in the proportion of individuals emigrating (arcsine transformed) and the numbers of immigrants in each treatment using one-way analyses of variance for each species. Emigration was calculated by dividing the number of marked individuals present at the end of the experiment by the number added at the beginning of the experiment. The number of immigrants was simply the number of unmarked adults present in treatment patches at the end of the experiment. These response variables were quantified differently because while the number of immigrants was potentially unlimited, the number of emigrants could only be as high as the number of frogs initially present (which varied by treatment).

Field data from 2000, 2001 and 2002 on the distribution of *M. bicalcaratus* and *M. punctatus* were analysed in two ways. First, I enumerated the number of *Pandanus* plants occupied in each year by *M. bicalcaratus* only, *M. punctatus* only and those plants occupied by both species. I then tested whether either species was more likely to occur alone than expected by chance using a chi-square test with Yates correction. Second, I examined the number of years a plant was occupied by both species relative to those occupied by only a single species. Using another chi-square test, this tested the hypothesis that extinction rates are higher in plants occupied by both species. All statistical tests were carried out in Systat 9.0 (Systat Inc., Evanston, IL, USA). Unless otherwise noted, means are presented (± SD).

## RESULTS

### Larval competition experiment

Larval growth rates varied significantly among treatments for both *Mantidactylus punctatus* (ANOVA  $F_{5,11} = 26.2$ ,  $P < 0.001$ ) and *M. bicalcaratus* (ANOVA  $F_{5,11} = 67.9$ ,  $P < 0.001$ ; Table 1). In treatments with



**Figure 1.** Average growth (mm  $\pm$  SD) of *Mantidactylus bicalcaratus* (open bars) and *M. punctatus* larvae (solid bars) in microcosm experiments over 22 d. Density combinations are as follows: (A) Species together with 4 *M. bicalcaratus*, 4 *M. punctatus*, (B) Species together with 4 *M. bicalcaratus*, 8 *M. punctatus*, (C) Species together with 8 *M. bicalcaratus*, 4 *M. punctatus*, (D) Species alone at a density of 12 larvae per container, (E) Species alone at a density of 8 larvae per container, (F) Species alone at a density of 4 larvae per container. See Table 1 for additional details.

only conspecifics, intraspecific competition significantly reduced growth rates in both species (Table 1, Figure 1). For *M. punctatus*, the growth rates in the heterospecific treatments were not significantly different from the growth rates in the conspecific treatments at the same density (Table 1, Figure 1). For *M. bicalcaratus*, however, growth rates in the heterospecific treatments were significantly lower than in conspecific treatments at the same density (Table 1, Figure 1). Survivorship over the course of the experiment ranged from 84.4% to 100% for both species, and no significant differences in survivorship were detected in any treatments ( $F_{11,24} = 0.973$ ,  $P = 0.493$ ).

As was found in earlier experiments (Lehtinen 2004), *M. bicalcaratus* larvae had faster growth rates than *M. punctatus* larvae in the presence of conspecifics (Table 1, Figure 1). However, *M. bicalcaratus* exhibited reduced growth rates in the presence of *M. punctatus* by 0.08–0.23 mm d<sup>-1</sup> compared with growth rates in treatments with only conspecifics at the same density (two-way ANOVA  $F_{1,12} = 23.4$ ,  $P < 0.001$ ; Table 4). This is a 19–33% decrease in daily growth rates in the presence of *M. punctatus*. In contrast, *M. punctatus* did not have its growth rates significantly reduced in the presence of *M. bicalcaratus*, in fact, they were slightly enhanced (up to 0.04 mm d<sup>-1</sup>, an 11% increase relative to growth rates with conspecifics; Table 4). Based on these data,

**Table 4.** Differences in mean growth rates (mm d<sup>-1</sup>) of *Mantidactylus bicalcaratus* (*bic*) and *M. punctatus* (*pun*) larvae when with heterospecifics compared with when alone. Each treatment was replicated three times. A two-way ANOVA (with treatment and species as factors) indicated significantly different growth rates among species ( $P < 0.0001$ ).

Mean growth difference (mm d <sup>-1</sup> )	Treatment		
	8 <i>bic</i> /4 <i>pun</i>	4 <i>bic</i> /4 <i>pun</i>	4 <i>bic</i> /8 <i>pun</i>
<i>M. bicalcaratus</i>	-0.079	-0.228	-0.101
<i>M. punctatus</i>	0.005	0.044	0.027

the per capita competitive effect of *M. punctatus* larvae on *M. bicalcaratus* larvae (i.e. the competition coefficient) is 1.5 (0.68/0.452; Table 1). The per capita competitive effect of *M. bicalcaratus* on *M. punctatus* is 0.9 (0.399/0.443; Table 1).

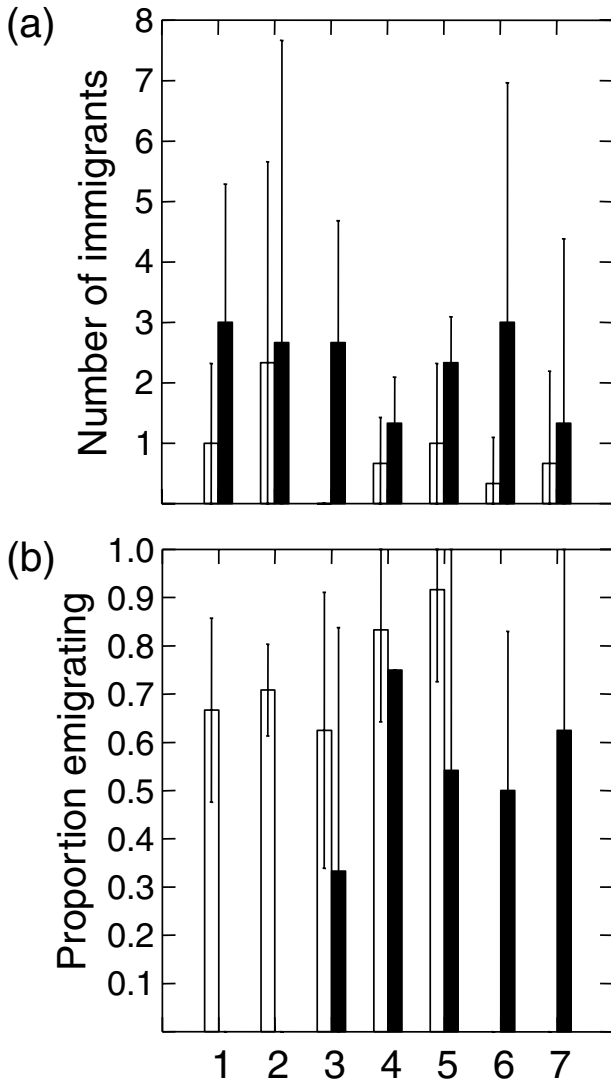
### Adult addition experiment

The results of the addition experiment with adult *M. bicalcaratus* and *M. punctatus* were much less clear. The data indicate very high levels of emigration for both species (overall mean proportion emigrating 0.75 for *M. bicalcaratus* and 0.55 for *M. punctatus*), much higher than those found in unmanipulated *Pandanus*. Emigration did not differ significantly among treatments for either species (*M. bicalcaratus* ANOVA  $F_{4,10} = 2.23$ ,  $P = 0.139$ ; *M. punctatus* ANOVA  $F_{4,10} = 0.73$ ,  $P = 0.490$ ). In treatments involving both species, *M. bicalcaratus* emigration was always higher than *M. punctatus* (mean proportion  $0.79 \pm 0.20$  and  $0.54 \pm 0.33$  – a non-significant difference with a two-sample t-test ( $t = 2.02$ ,  $P = 0.066$ ); Table 3, Figure 2).

The number of immigrants of *M. bicalcaratus* and *M. punctatus* also did not differ among treatments (*M. bicalcaratus* ANOVA  $F_{6,14} = 1.12$ ,  $P = 0.400$ ; *M. punctatus* ANOVA  $F_{6,14} = 0.32$ ,  $P = 0.919$ ). Again, however, if we examine immigration by *M. bicalcaratus* in treatments with and without *M. punctatus*, there is a trend for immigration to be higher where *M. punctatus* is absent (median number of immigrants per patch in treatments with *M. punctatus*: 0 (range 0–2); without *M. punctatus*: 1.5 (range 0–5); Mann–Whitney test,  $U = 16.5$ ,  $P = 0.186$ ). These trends notwithstanding, this experiment provided no unequivocal evidence of competitive interactions among adults of these two species.

### Field distribution

Chi-square tests indicate that *M. bicalcaratus* was significantly more likely to occur in the absence of *M. punctatus* than in its presence (for all years,  $\chi^2 > 11.9$ ,  $df = 1$ ,  $P < 0.001$ ; Table 5). Similarly, *M. punctatus* was significantly more likely to occur in the presence of

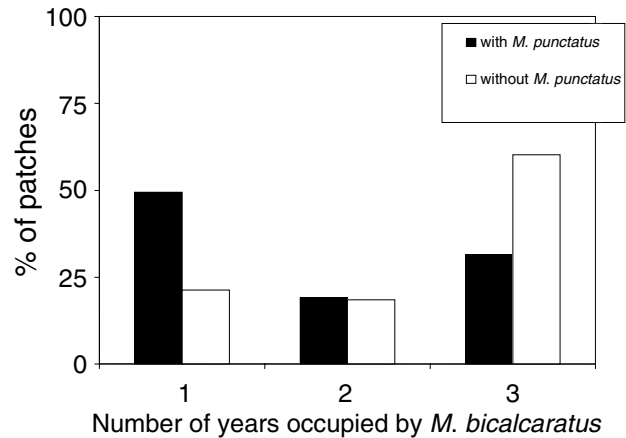


**Figure 2.** (a) Proportion of transplanted adults emigrating ( $\pm$  SD; *Mantidactylus bicalcaratus* open bars, *M. punctatus* solid bars). Treatments 1 and 2 were *M. bicalcaratus* alone at low and high density, respectively. Treatment 3 was 8 *M. bicalcaratus* and 4 *M. punctatus*. Treatment 4 was 4 adults of each species and treatment 5 was 8 *M. punctatus* and 4 *M. bicalcaratus*. Treatments 6 and 7 were *M. punctatus* alone at high and low density, respectively. No significant differences were detected. (b) Number of adult immigrants arriving at treatment patches at 10 d post-transplantation ( $\pm$  SD; *M. bicalcaratus* open bars, *M. punctatus* solid bars, same treatment labels as above). No significant differences were detected. See Table 3 for description of treatments.

*M. bicalcaratus* than in its absence (for all years,  $\chi^2 > 27.5$ ,  $df = 1$ ,  $P < 0.001$ ; Table 5). For *M. bicalcaratus*, plants with *M. punctatus* present were significantly less likely to be occupied in multiple years ( $\chi^2 = 12.4$ ,  $df = 2$ ,  $P < 0.01$ ; Figure 3). For plants where *M. punctatus* was absent, *M. bicalcaratus* was significantly more likely to be present in multiple years ( $\chi^2 = 71.9$ ,  $df = 2$ ,  $P < 0.001$ ; Figure 3).

**Table 5.** Number of unoccupied patches and those occupied by *Mantidactylus bicalcaratus* (*bic*) alone, *M. punctatus* (*pun*) alone and both species together (2000–2002,  $n = 281$ ). P values indicate chi-square test results.

Year	Both present	<i>M. bic</i> only	<i>M. pun</i> only	Both absent	P
2000	61	147	1	72	< 0.001
2001	53	108	4	116	< 0.001
2002	53	95	11	122	< 0.001



**Figure 3.** Stability of *Mantidactylus bicalcaratus* populations in the presence (solid bars) and absence (open bars) of *M. punctatus*, 2000–2002.

No similar analysis was possible for *M. punctatus* as few plants contained only *M. punctatus*.

**DISCUSSION**

In organisms with complex life histories, competition may act in one or more life stages or not at all. I have experimentally shown that there is strong, asymmetric competition between the larvae of *Mantidactylus bicalcaratus* and *M. punctatus*, with *M. punctatus* being the superior competitor under the conditions examined. Large differences in the per capita competitive effect (0.9 vs. 1.5) suggest that these results are both statistically and biologically significant. The conditions in the plastic bottles used in this experiment are quite comparable to *Pandanus* leaf axils (see Lehtinen 2004), so these results should apply to tadpoles in the field. Field experiments with adults showed no conclusive evidence of a similar competitive effect. However, even if interspecific competition acts only in the larval stage of these frogs, this still might be manifested in the distribution and abundance of adults. For example, breeding habitat choice in adult *M. bicalcaratus* should favour *Pandanus* plants where *M. punctatus* is currently absent, since its larvae are at a competitive disadvantage in the presence of this species.

It is possible that the adults of these two species do currently compete but my experiments were unable to detect a competitive effect. A variety of factors could have obscured clear evidence of competition. For example, uncontrolled natural variation among replicates may have played a part. While every attempt was made to assemble comparable replicates, the natural heterogeneity of the *Pandanus* plants used, made some differences unavoidable (Table 2). These differences may have altered the suitability of the plants for one or the other species or influenced the immigrant pool. While field experiments are often more realistic than those done in the laboratory (Skelly 2002), they clearly also offer much less control over the many potentially confounding factors.

Site fidelity was another probable source of variation in the field experiment with adults. The high levels of emigration observed in transplanted frogs likely resulted at least partially from attempts to return to a favoured area. Many amphibians are known to be able to return to preferred sites after displacement (Crump 1986, McVey *et al.* 1981, Twitty *et al.* 1967), and subsequent experiments in this system confirmed that both species do often return to particular *Pandanus* plants after being displaced (unpubl. data). Lastly, the high variability in response variables in this experiment combined with low levels of replication may simply not have provided enough statistical power to detect any trends that were present.

In the experiment with larvae, however, strong asymmetric competition was clearly demonstrated. Several lines of evidence make it likely that the observed competitive effect was due to exploitative interactions. First, no obvious interference behaviour of either adults or larvae was noted despite many hours of observations. Second, there were no significant differences in larval survivorship among treatments, as might be expected with an interference mechanism. Third, in these aquatic microcosms, food is likely to be limiting, and in other experiments with these larvae intraspecific competition was reduced in the presence of high levels of food (Lehtinen 2004; see also Jungfer 1996, Schiesari *et al.* 2003). Lastly, in general, others who have studied anuran larvae have not found interference competition to be common (Morin & Johnson 1988, Petranka 1989). While these lines of evidence may be somewhat convincing, only further experiments can elucidate the mechanisms of the competitive interactions between larvae of these species. Which particular traits in *M. punctatus* tadpoles lead to superior competitive ability is also unknown.

### Consequences for ecological theory

The idea that asymmetric competitive interactions among species can influence population dynamics has long

been of interest to theoreticians (Hanski & Zhang 1993, Horn & MacArthur 1972, Levins & Culver 1971). While a great number of empirical studies have demonstrated interspecific competition in diverse taxa, to my knowledge, only one study has clearly demonstrated that it can influence local extinction rates in natural populations. Bengtsson (1989; see also Bengtsson 1993) provided evidence for elevated extinction rates in water flea (*Daphnia*) populations when multiple species were present (presumably when interspecific competition was strong). Data from field distributions of *M. bicalcaratus* and *M. punctatus* revealed many cases where both species were present in the same *Pandanus* plant at the same time. However, statistical analyses demonstrated that *M. bicalcaratus* (the inferior larval competitor) was significantly less likely to occur in the presence of *M. punctatus* (the superior larval competitor) than alone (Table 5). Additionally, *M. bicalcaratus* populations occupying plants with *M. punctatus* had significantly higher extinction rates than those in plants where *M. bicalcaratus* was found alone (Figure 3). The present study then, provides a second example of the influence of competitive interactions on population dynamics.

These frogs coexist sympatrically at Sainte Luce and at many other sites in the eastern rain forest belt of Madagascar. If competition is strong and asymmetric, how then does coexistence come about? In the *Daphnia* example, the fugitive mechanism (Hutchinson 1951) has been suggested as a likely mechanism of coexistence. In this scenario, the inferior competitor (the fugitive species) is a superior disperser and can thereby coexist with a superior competitor via a competition–colonization trade-off (Yu & Wilson 2001). Mark–recapture data from these frogs suggest that *M. bicalcaratus* is a superior disperser relative to *M. punctatus* (unpubl. data), therefore the fugitive mechanism may be at work in this system. The negative effect of *M. punctatus* on *M. bicalcaratus* also helps explain the occupancy of very low quality sink habitats by *M. bicalcaratus* (Lehtinen 2003a). Other plausible coexistence mechanisms in this system include niche partitioning and a trade-off between competitive ability and fecundity. Future work will assess these and other potential mechanisms allowing coexistence of these sympatric competitors. At other sites in the eastern rain-forest belt of Madagascar, at least five species of obligate *Pandanus*-dwelling *Mantidactylus* coexist. These areas may provide opportunities to further investigate competition and coexistence among a more diverse set of species.

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## LITERATURE CITED

- ALFORD, R. A. 1999. Ecology. Pp. 240–278 in McDiarmid, R. W. & Altig, R. (eds.). *Tadpoles: the biology of anuran larvae*. University of Chicago Press, Chicago.
- BENGTSSON, J. 1989. Interspecific competition increases local extinction rate in a metapopulation system. *Nature* 340:713–715.
- BENGTSSON, J. 1993. Interspecific competition and determinants of extinction in experimental populations of three rockpool *Daphnia* species. *Oikos* 67:451–464.
- BLAUSTEIN, L. & MARGALIT, J. 1994. Mosquito larvae (*Culicoides longiareolata*) prey upon and compete with toad tadpoles (*Bufo viridis*). *Journal of Animal Ecology* 63:841–850.
- BROWN, J. H. & DAVIDSON, D. W. 1977. Competition between seed eating rodents and ants in desert ecosystems. *Science* 196:880–882.
- CONNELL, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122:661–696.
- CRUMP, M. L. 1986. Homing and site fidelity in a neotropical frog *Atelopus varius* (Bufonidae). *Copeia* 1986:438–444.
- DONNELLY, M. A., GUYER, C., JUTERBOCK, J. E. & ALFORD, R. A. 1994. Techniques for marking amphibians. Pp. 277–284 in Heyer, W. R., Donnelly, M. A., McDiarmid, R. W., Hayek, L.-A. C. & Foster, M. S. (eds.). *Measuring and monitoring biodiversity: standard methods for amphibians*. Smithsonian Institution Press, Washington, DC.
- GLAW, F. & VENCES, M. 1994. *A field guide to the amphibians and reptiles of Madagascar*. (Second edition). Moos Druck, Leverkusen. 480 pp.
- GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183–190.
- HAIRSTON, N. G. 1980. The experimental test of an analysis of field distributions: competition in terrestrial salamanders. *Ecology* 61:817–826.
- HANSKI, I. & ZHANG, D. Y. 1993. Migration, metapopulation dynamics and fugitive coexistence. *Journal of Theoretical Biology* 163:491–504.
- HORN, H. S. & MACARTHUR, R. H. 1972. Competition among fugitive species in a harlequin environment. *Ecology* 53:749–752.
- HUTCHINSON, G. E. 1951. Copepodology for the ornithologist. *Ecology* 32:571–577.
- INGER, R. F. & GREENBERG, B. 1966. Ecological and competitive relations among three species of frog (genus *Rana*). *Ecology* 47:746–759.
- JUNGFER, K.-H. 1996. Reproduction and parental care of the coronated treefrog, *Anothea spinosa* (Steindachner, 1864) (Anura: Hylidae). *Herpetologica* 52:25–32.
- LEHTINEN, R. M. 2002. The use of screw pines (*Pandanus* spp.) by amphibians and reptiles in Madagascar. *Herpetological Bulletin* 82:20–25.
- LEHTINEN, R. M. 2003a. *Ecology and metapopulation dynamics of two Pandanus-dwelling frogs from Madagascar*. Ph.D. Thesis. University of Michigan, Ann Arbor. 260 pp.
- LEHTINEN, R. M. 2003b. Parental care and reproduction in two species of *Mantidactylus* (Anura: Mantellidae). *Journal of Herpetology* 37:766–768.
- LEHTINEN, R. M. 2004. Tests for competition, cannibalism and priority effects in two phytotelm-dwelling tadpoles from Madagascar. *Herpetologica* 60:1–13.
- LEHTINEN, R. M., RICHARDS, C. & NUSSBAUM, R. A. 2004. Evolution of a complex reproductive trait: phytotelm breeding in mantellid frogs from Madagascar. Pp. 45–53 in Lehtinen, R. M. (ed.). *Ecology and evolution of phytotelm breeding anurans*. Miscellaneous Publications of the University of Michigan Museum of Zoology. No. 193.
- LEVINS, R. & CULVER, D. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences (USA)* 68:246–248.
- MCVEY, M. E., ZAHARY, R. G., PERRY, D. & MACDOUGAL, J. 1981. Territoriality and homing behavior in the poison dart frog (*Dendrobates pumilio*). *Copeia* 1981:1–8.
- MORIN, P. J. & JOHNSON, E. A. 1988. Experimental studies of asymmetric competition among anurans. *Oikos* 53:398–407.
- PETRANKA, J. W. 1989. Chemical interference competition in tadpoles: does it occur outside laboratory aquaria? *Copeia* 1989:921–930.
- SCHIESARI, L., GORDO, M. & HÖDL, W. 2003. Treeholes as calling, breeding, and developmental sites for the Amazonian canopy frog, *Phrynohyas resinifictrix* (Hylidae). *Copeia* 2003:263–272.
- SCHOENER, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* 122:240–285.
- SKELLY, D. K. 2002. Experimental venue and estimation of interaction strength. *Ecology* 83:2097–2101.
- TOKESHI, M. 1999. *Species coexistence: ecological and evolutionary perspectives*. Blackwell Science, Oxford. 294 pp.
- TWITTY, V. C., GRANT, D. & ANDERSON, O. 1967. Long distance homing in the newt *Taricha rivularis*. *Proceedings of the National Academy of Sciences (USA)* 50:51–58.
- WERNER, E. E. 1994. Ontogenetic scaling of competitive relations: size-dependent effects and responses in two anuran larvae. *Ecology* 75:197–213.
- YU, D. W. & WILSON, H. B. 2001. The competition–colonization trade-off is dead; long live the competition–colonization tradeoff. *American Naturalist* 158:49–63.