The natural history of two plant-breeding frogs from Madagascar, *Guibemantis bicalcaratus* and *G. punctatus* (Anura: Mantellidae)

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Abstract. The mantelline frogs *Guibemantis bicalcaratus* and *G. punctatus* were described in 1913 and 1979, respectively, yet little information has previously been available about their biology. These species breed in the water-filled leaf axils of *Pandanus* or other water-holding plants in the rainforests of eastern Madagascar. I conducted a mark-recapture study in a fragment of littoral rainforest from 2000-2002 to study these plant-breeding frogs. Mark-recapture data from 567 *G. bicalcaratus* and 284 *G. punctatus* indicate that both species have a short life span (< 12 months in *G. bicalcaratus*, < 14 months in *G. punctatus*) and have significantly female-biased sex ratios (0.371 for *G. bicalcaratus* and 0.307 for *G. punctatus*). On average, 69.6 % (*G. bicalcaratus*) and 65.0 % (*G. punctatus*) of the post-metamorphic population were sexually mature adults. For both species, the percentage of sexually mature adults was highest at the beginning of the rainy season (up to 95%) and lowest towards the end (as low as 50%), as metamorphosing tadpoles emerged as juveniles. At metamorphosis, juveniles of both species are about 9 mm SVL. *Guibemantis bicalcaratus* attains sexual maturity at approximately 16 mm SVL and females are significantly larger than males (p < 0.001). *Guibemantis punctatus* attains sexual maturity at a somewhat larger size (18 mm SVL) and there is no sexual size dimorphism (p = 0.58). Observations on microhabitat use suggest some niche partitioning, with *G. punctatus* found significantly more frequently in the leaf axils with the most water. These microhabitat differences may be important in allowing the local coexistence of these sympatric habitat specialists.

Key words. Activity patterns, body size, longevity, mark-recapture, population structure, sex ratio, sexual dimorphism.

Introduction

Ongoing studies of the endemic amphibians of Madagascar have revealed a diverse and unique fauna now numbering well over 200 species (Glaw & Vences 2003). However, while our knowledge of the number and identity of species from Madagascar continues to grow, there is yet very little detailed information on the ecology or natural history of most species. A good example are the *Pandanus*-breeding frogs in the genus *Guibemantis*, subgenus *Pandanusicola* (Mantellidae). This group currently includes five species that breed in the water-filled leaf axils of *Pandanus* or other water-holding plants (*G. albolineatus, G. bicalcaratus, G. flavobrunneus, G. pulcher,* and *G. punctatus*) and one

that breeds in ponds (*G. liber*; Glaw & Vences 2006).

Guibemantis bicalcaratus was described by Boettger in 1913 and *G. punctatus* by Blommers-Schlösser in 1979, yet almost no details on the biology of this species are available beyond brief descriptions in field guides (Glaw & Vences 1994) or systematic works (Blommers-Schlösser 1979, Blommers-Schlösser & Blanc 1991). Recently, a few papers on the parental care (Lehtinen 2003) and tadpole ecology of these species have appeared (Lehtinen 2004, 2005) and an earlier paper (Razahelisoa 1974) provided some basic information on the larval development of *G. bicalcaratus*. However, no other studies of these interesting frogs are available. To provide basic natural history information on

these plant-breeding frogs, I conducted ecological studies of *G. bicalcaratus* and *G. punctatus* from 2000-2002 at a site in southeastern Madagascar.

Herein, I provide the first detailed data on sexual size dimorphism, size at maturity, longevity, population structure, sex ratios and activity patterns in these species.

Materials and methods

The study area is located in a remnant littoral rainforest (~ 450 ha) approximately 1.5 km west of the village of Sainte Luce (Manafiafy), Tolagnaro fivondronana, Toliara province in southeastern Madagascar (24°46'S; 47°10'E). This area is near the very southernmost extent of rainforest in Madagascar. Littoral rainforest is a relatively rare subtype of Malagasy rainforest found only on sandy soils along the coasts at low elevations (Goodman et al. 1997). Canopy height is normally 10–12 m with a few emergent trees up to 15 m. Annual precipitation in this area has been reported from 1500 to over 2600 mm (Pulian et al. 1973, Donque 1975; R. Heriarivo pers. comm.) with most rainfall occurring in the hot, rainy season (late November to late March or early April). Substantial rain can also fall in the 'dry season' and while little breeding activity has been reported, many frogs are still active during this time. For more detailed information on the study area, see Lehtinen et al. (2003).

Three *Pandanus*-breeding frogs in the genus *Guibemantis* (Mantellidae: *G. bicalcaratus, G.* cf. *pulcher, G. punctatus*) occur sympatrically at Sainte Luce. However, *G.* cf. *pulcher* was rarely encountered and I have little data on this species. Also, while I will use the binomial *G. bicalcaratus* throughout this paper, recent evidence suggests that specimens attributed to *G. bicalcaratus* from southeastern Madagascar may be a different species than the one found in the highlands, based on a phylogenetic analysis of mitochondrial DNA sequences (Lehtinen et al. 2007). At this study site, these species are restricted to rainforest and are found only in and on *Pandanus* plants ("screw pines"), where they complete their entire life cycle. A large *Pandanus* plant may be 4 m in width with a hundred or more conically-shaped leaf axils, which may each contain up to about 200 mL of rainwater. However, only a small fraction of these leaf axils usually contain a suitable amount of water for breeding purposes and most plants are much smaller.

Observations on *G. bicalcaratus* and *G. punctatus* (Fig. 1) were made in the Sainte Luce rainforest during the rainy seasons of 2000, 2001 and 2002. Three 125 × 75 m permanent forest plots were established and the spatial locations of all *Pandanus* plants were mapped out (hereafter referred to as Plots 1, 2 and 3). Each individual plant (n = 839) was surveyed for frogs three times in each year of the study (7,551 plant surveys total in all three years). Surveys involved visually examining all leaves and leaf axils in each plant for frogs. I searched as long as was necessary to minimize the possibility of missing any frogs (usually less than ten minutes per plant). These small frogs are conspicuously colored, 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. Most *Pandanus* plants were found on the forest floor; however, some ascend into the canopy. *Pandanus* plants whose height was greater than 1.5 m but less than 4.0 m were sampled using a stepstool constructed for this purpose. Plants higher than 4.0 m were sampled (when possible) by climbing adjacent trees using the single rope climbing technique (Laman 1995). Surveys took place between 0600 and 1700 h during the height of the rainy season (early January to late March).

Population densities were calculated by dividing the density of frogs in a plot by the plot size. As advocated by Wilson & Hardy

(2002), sex ratios were calculated by dividing the number of marked males (as defined below) by the total number of marked adults. In this scheme, 1:1 sex ratios would be equal to 0.5 and male and female biased populations would be greater than and less than 0.5, respectively. The percentage of the population that was sexually mature was calculated with pooled data from visual surveys. Egg clutches from *G. punctatus* were collected and reared in plastic bottles in a field laboratory to observe development.

In Plots 1 and 2, frogs were uniquely marked using toe-clipping (Donnelly & Guyer 1994). Upon capture, all frogs were sexed and measured (snout-vent length = SVL) with calipers to the nearest millimeter. Males of both species were distinguished from females by a combination of the presence of femoral glands on the ventral surface of the thigh and/or by whitish coloration of the paired, subgular vocal sacs. Adult males were distinguished from juveniles by these same features. Previous descriptions of the vocal sacs of these species as single subgular (Glaw & Vences 1994) may refer to other species or be erroneous. The smallest gravid females of *G. bicalcaratus* and *G. punctatus* that I found were 18 mm SVL, therefore, adult females were distinguished from juveniles arbitrarily by this size threshold. Gravid females were identified by looking for eggs through the semi-transparent body wall.

Activity patterns were quantified in 2002 by repeatedly visiting ten particular *Pandanus* plants on eight days over a 14 day period (15-28 February). On each sampling day, each plant was visited in early morning (0600–0715 h), the middle of the day (1100–1330 h) and in the late afternoon (1715–1815 h). At each visit, the detailed spatial locations of individual frogs on each plant were noted. Plants were not sampled after dark because other observations indicated that these species are not very active at night. Each plant visit was limited to a maximum of three minutes to minimize the influence of observer disturbance. The spatial location of each frog found was described on each visit in the fol-

lowing way: (i) the relative location of each frog on each plant was quantified as low (in the lowest leaves or leaf axils), medium (in the middle leaves or leaf axils) or high (in the highest leaves or leaf axils), (ii) each frog was described as being located out on a leaf or inside a leaf axil and (iii) the leaf axil nearest to the frog's location on the plant was described as full, partially full, or empty of rainwater. Only adult frogs were used to collect spatial location data. Each plant was visited eight times in the morning, eight times in the middle of the day, and eight times in the late afternoon for a total of 24 visits per plant (240 visits total)

Non-parametric Kruskal-Wallis tests were used to make inter- and intra-specific comparisons on the spatial locations of frogs. Two-sample *t*-tests were used to assess interspecific and intersexual size dimorphism. *G* tests for goodness-of-fit were used to examine departures from a 1:1 sex ratio. Mean values are presented in the text with the standard deviation.

Results
Tadpoles

Larvae of both species could be found in a single *Pandanus* plant and, on several occasions, were found to co-occur in the same leaf axil. More frequently, however, when larvae were found in a leaf axil, it contained only one species. Natural densities of larvae per *Pandanus* axil varied from one to 22, with the average being seven. Up to three cohorts of different sizes were commonly found in the same axil together. On several occasions I observed larvae of *Guibemantis bicalcaratus* and *G. punctatus* crawling along the leaf surface to move to a different leaf axil, possibly in response to drying conditions. Recent metamorphs (with tail bud still present) averaged 8.5 ± 1.6 mm SVL (*G. bicalcaratus*, n = 17) and 9.1 ± 1.4 mm SVL (*G. punctatus*, n = 16). See Appendix for notes on early embryonic and larval development of *G. punctatus*.
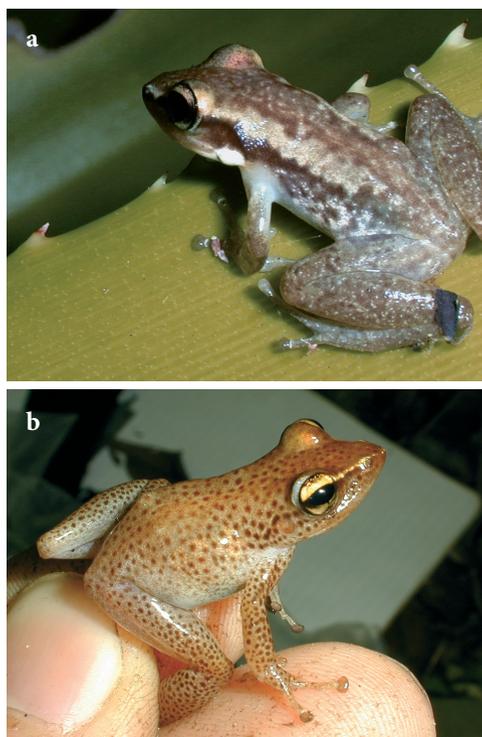
Fig. 1. (a) Adult male *Guibemantis bicalcaratus* positioned on the edge of a *Pandanus* leaf. (b) Adult female *G. punctatus*.

Activity patterns and microhabitat use

Guibemantis punctatus was equally likely to be found in leaves low, high or in the middle of the plant, regardless of the time of day (Fig. 2a; p > 0.4). However, *G. punctatus* was significantly more likely to be found in water-filled axils than *G. bicalcaratus* (Fig. 2a; p < 0.001). *G. punctatus* showed a peak of activity during the early morning with a smaller peak in the late afternoon (Fig. 2a; p < 0.001) when adults were out on the leaves foraging and seeking mates. During the hot mid-day hours, *G. punctatus* was most often found hidden in water-filled leaf axils.

Guibemantis bicalcaratus adults were also equally likely to be found in leaves low, high or in the middle of the plant, regardless of time of day (Fig. 2b; p > 0.5). This species was also randomly distributed relative to water levels in leaf axils and these patterns also did not vary based on time of day (Fig. 2b. p > 0.05). However, *G. bicalcaratus* was much more likely to be out on the leaves early in the morning than later in the day (Fig. 2b; p < 0.001).

Intersexual and interspecific size dimorphism

Significant differences were found in the size of *Guibemantis bicalcaratus* females (mean = 23.1 ± 2.3 mm SVL; n = 324; Fig. 3) and males (mean = 20.7 ± 1.5 mm SVL; n = 200; p < 0.001; Fig. 3), but not between *G. punctatus* females (21.0 ± 2.2 mm SVL; n = 146; Fig. 4) and males (mean = 21.0 ± 1.2 mm SVL; n = 64; p = 0.91; Fig. 4). Interspecific differences in size were also noted with females of *G. bicalcaratus* being significantly larger than females of *G. punctatus* (p < 0.001) and males of *G. punctatus* being larger than males of *G. bicalcaratus* (p = 0.024). Juveniles of *G. punctatus* (mean = 14.3 ± 1.9 mm SVL; n = 78) were significantly larger than those of *G. bicalcaratus* (13.4 ± 1.7 mm SVL; n = 54; p < 0.001). The minimum size at maturity for males (based on the appearance of secondary sexual characteristics) was 16 and 18 mm SVL for *G. bicalcaratus* and *G. punctatus*, respectively.

Lifespan, population structure and sex ratio

In three rainy seasons at Sainte Luce, 567 *Guibemantis bicalcaratus* were uniquely marked using toe-clipping. Three hundred and five of these individuals were subsequently recaptured (53.8 %), but no inter-year recaptures were recorded. Two hundred eighty-four *G. punctatus* were uniquely marked during the same period. Ninety-five individuals were recaptured (33.5 %) includ-
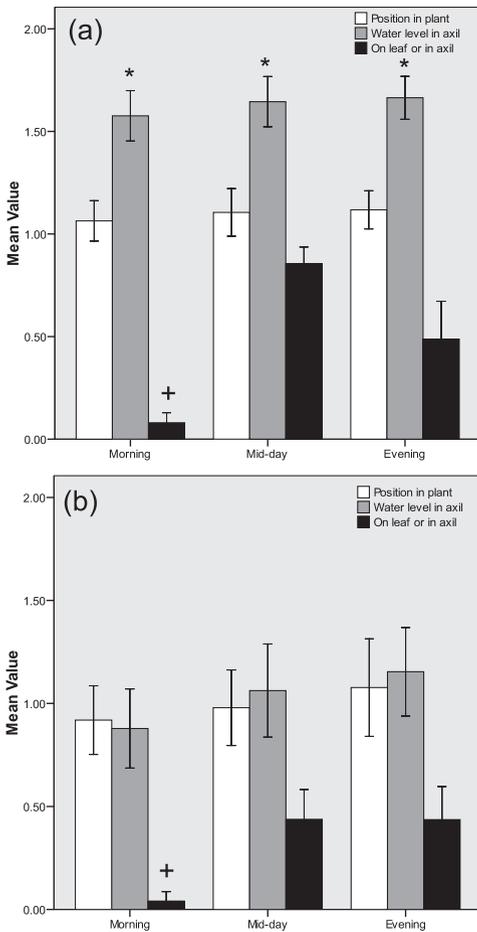
Fig. 3. Distribution of body sizes of adult female (unshaded bars, n = 324) and adult male (shaded bars, n = 200) *Guibemantis bicalcaratus*.

Fig. 2. Activity patterns of *Guibemantis punctatus* (a) and *G. bicalcaratus* (b). Relative position of each frog was quantified as low (0), medium (1) or high (2) in the plant. Water level in the nearest leaf axil to each frog's location was quantified as empty (0), half-full (1) or full (2). Specific position of each frog was described as on the leaf (0) or in the leaf axil (1). Mean values ± 2 SE are presented. + = significant difference within species. * = significant difference between species (using Kruskal-Wallis rank-based tests).

ing two inter-year recaptures. These inter-year recaptures were marked as juveniles near the end of one rainy season and recaptured as very large females at the beginning of the following rainy season. Clipped toes were clear-
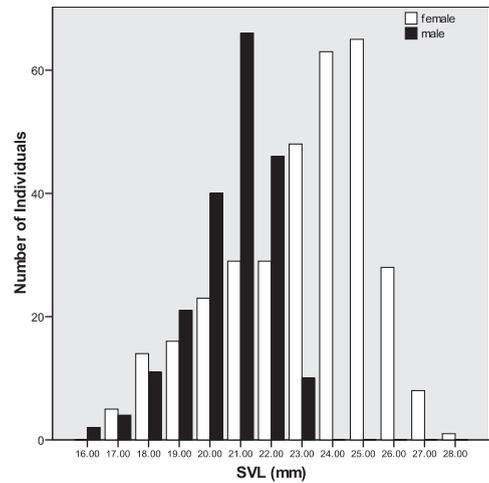
ly visible throughout the study period and no regeneration was noted in captive animals.

On average, sexually mature adults represented 69.6 % (range: 60.0–86.5%) and 65.0 % (range: 49.5–95.3%), respectively, of the total post-metamorphic population of *G. bicalcaratus* and *G. punctatus* at Sainte Luce (Fig. 5). However, there were consistently more juveniles present (as a proportion of the total post-metamorphic population) later in the rainy season compared to the beginning (Fig. 5). Population density (of post-metamorphic individuals) averaged 0.0091/m² ± 0.0085 (range: 0–0.0512/m²) for *G. bicalcaratus* and 0.0063/m² ± 0.011 (range: 0–0.04/m²) for *G. punctatus*. On a per plant basis, density of post-metamorphic individuals averaged 2.0 ± 1.29 individuals per occupied *Pandanus* plant (range: 1–10) for *G. bicalcaratus* and 3.4 ± 3.4 individuals per occupied *Pandanus* plant (range: 1–18) for *G. punctatus*.

Data from all plots and years indicate a significantly female-biased sex ratio for both species (0.371 for *G. bicalcaratus* p < 0.001; 0.307 for *G. punctatus*, p < 0.001; Table 1). While the sex ratio for both species was always female-biased, the strength of this bias varied among years and plots (Table 1).
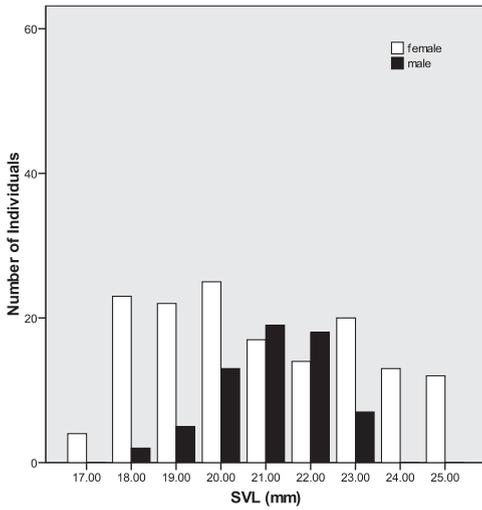
Fig. 4. Distribution of body sizes of adult female (unshaded bars, n = 146) and adult male (shaded bars, n = 64) *Guibemantis punctatus*.

Discussion
Sex ratio

Although the sex ratio was variable both among years and plots, on average in this population, females heavily outnumbered males in *Guibemantis bicalcaratus* and *G. punctatus* (Table 1). In most anurans that have been studied, a 1:1 sex ratio (e.g. *Hyla rosenbergi:* Kluge 1981; *Litoria aurea:* Greer & Byrne 1995) or a male biased one (e.g. *Ranidella riparia, R. signifera:* Odendaal &

Iwasa 1987; *Rana sylvatica:* Berven 1990) has been found. Only a few studies have reported female-biased sex ratios (e.g. *Rana pretiosa*: Turner 1962; *Dendrobates pumilio*: Pröhl 2002). The one other mantellid species for which sex ratio data are available (*Boehmantis microtympanum*) has approximately equal number of males and females (Andreone 1998).

This female-biased pattern in *G. bicalcaratus* and *G. punctatus* could result from differential capture probabilities, but my field observations suggest that males are not more difficult to capture than females. Also, since the breeding and non-breeding habitat is identical in these species, it is unlikely that my sex ratio estimates are biased by differences in residence time at breeding sites or differential microhabitat use among the sexes. Blommers-Schlösser (1979) suggested that in some *Guibemantis*, femoral glands may only occur seasonally (i.e. during the breeding season). If this were the case, adult males lacking obvious secondary sexual characteristics could have been misclassified as females. However, sexually mature males of both species never lost obvious femoral glands or vocal sac coloration in over one month in captivity (unpublished data) and all my work was conducted during the rainy season, so it is unlikely that this biased my sex ratio estimates. While the mechanism generating this female biased sex ratio is unknown, differences in survivorship among the sexes

Tab. 1. (i) Numbers of adult male and female *Guibemantis bicalcaratus* and *G. punctatus* caught at Sainte Luce. (ii) Sex ratios are given as the number of males divided by the total number of adults such that a 1:1 sex ratio would be 0.5. G-tests for goodness-of-fit were used only with pooled data from all years for each species to test for significant departures from a 1:1 sex ratio (significant differences indicated in bold, α = 0.05).

		plot 1 2000	plot 2 2000	both 2000	plot 1 2001	plot 2 2001	both 2001	plot 1 2002	plot 2 2002	both 2002	all plots, all years
G. bicalcaratus	(i)	42, 52	20, 32	62, 84	38, 81	24, 55	62, 136	39, 42	26, 58	65, 100	189, 320
	(ii)	0.447	0.385	0.425	0.319	0.304	0.313	0.481	0.310	0.394	**0.371**
G. punctatus	(i)	5, 8	9, 24	14, 32	2, 7	15, 23	17, 30	4, 17	27, 61	31, 78	62, 140
	(ii)	0.455	0.273	0.304	0.222	0.395	0.362	0.191	0.307	0.284	**0.307**

may be responsible. In a savanna area of West Africa, GRAFE et al. (2004) found that lack of rainfall affected male survival more than females in *Hemisus marmoratus*. While this may be unlikely for rainforest frogs, differential vulnerability to predators is one plausible mechanism. Previous observations suggest that both snakes and spiders prey heavily on these frogs (LEHTINEN 2002) and during the breeding season, vocalizing males are probably more conspicuous to predators than females. While environmental sex determination is currently unknown in amphibians, theoretically this mechanism could also generate biased sex ratios if environmental conditions favored the production of one sex over another. Information on sex ratios at metamorphosis would help provide a mechanism for this unusual pattern.

Body size patterns

Sexual size dimorphism is the norm in anurans, with females usually larger than males (SHINE 1979). In *Guibemantis bicalcaratus* (a prolonged, but not year-round breeder), larger female size (Fig. 4) may come about from a variety of factors. For example, selection may favor females that lay more eggs. Since clutch size is strongly correlated to body size, selection for increased clutch size would necessarily also favor the evolution of larger female body size (WOOLBRIGHT 1983). Being the limiting sex, male choice for larger females could also be driving size dimorphism in *G. bicalcaratus*. In a female-biased population and in the absence of territoriality and obvious male-male competition (unpublished data), sexual selection would likely not strongly favor large size in males. Alternatively, males may be smaller than females in *G. bicalcaratus* simply because opportunities for growth in males are limited after reaching sexual maturity due to high energetic expenditures in reproductive activities (WOOLBRIGHT 1983, 1989 but see SULLIVAN 1984). Also, if male survival probability is lower than that for fe-

males (as suggested above to explain the female biased sex ratio), fewer males would survive to a large body size. In contrast to *G. bicalcaratus*, *G. punctatus* does not exhibit any sexual dimorphism in size (Fig. 3). As both species inhabit the same environment, it is unclear why one species has sexually dimorphic body size while the other does not.

Interspecific size differences in males may result in part from different times to sexual maturity in the two species. Since secondary sexual characteristics appear at 16 mm SVL in *G. bicalcaratus* males these smaller individuals were counted as adults, thus reducing the average size. In *G. punctatus*, males up to 18 mm SVL were counted as juveniles, bringing up the mean size of both juveniles and adults. However, this does not explain the increased female body size in *G. bicalcaratus* compared to *G. punctatus* females (Figs. 3, 4). This larger body size in *G. bicalcaratus* females may explain the larger mean clutch size previously reported (LEHTINEN 2003).

Longevity

Mark-recapture data indicates that both species are short-lived. Intervals between field work at Sainte Luce were between 9 and 10 months, yet only two inter-year recaptures (both *Guibemantis punctatus* females) were noted out of 851 marked individuals. This is despite high within-year recapture rates (53.8 % and 33.5 %, for *G. bicalcaratus* and *G. punctatus*, respectively). If the maximum life span is around 12-14 months (including a 2-3 month larval period; LEHTINEN 2004), then the average life expectancy must be much lower and sexual maturity is obtained very rapidly. Further evidence for rapid maturity and a short life span includes the observation that sexually mature adults comprised a very high percentage of the total post-metamorphic population of *G. bicalcaratus* and *G. punctatus* (Fig. 5). At the beginning of the rainy season, nearly all of the individuals captured were sexually mature adults (Fig.
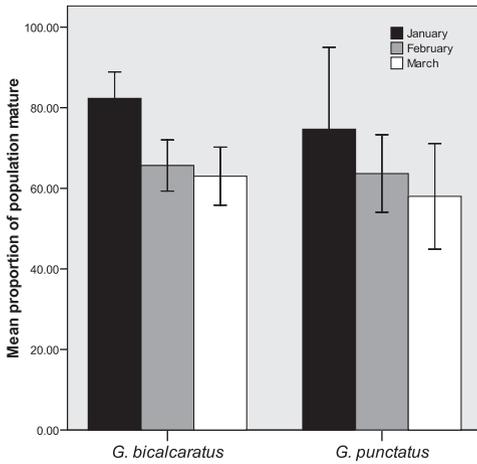
Fig. 5. Mean proportion of post-metamorphic population of *G. bicalcaratus* and *G. punctatus* that are sexually mature (2000-2002, error bars are ± 2 SE). Black, gray and clear bars indicate data from the first (January), second (February) and third (March) surveys in each year, respectively.

ation in density, trends in population density in this population were driven primarily by the availability of suitable *Pandanus* plants. In areas where suitable *Pandanus* were rare, *Guibemantis bicalcaratus* and *G. punctatus* were uncommon. In areas where suitable *Pandanus* were abundant, large numbers of *G. bicalcaratus* and *G. punctatus* were reliably found. Also, the proportion of juveniles in the population increased as the rainy season progressed (Fig. 5). This indicates that recruitment in these species is not continuous but rather driven by seasonal changes in precipitation. The first progeny from breeding at the onset of the rainy season (late November / early December) probably metamorphosed beginning in February. Most recruitment probably happens between February and May, although males have been occasionally heard calling after rain in drier months (J.-B. Ramanamanjato, pers. comm.).

5). These individuals likely feed and grow to maturity during the dry season (which is also spent in *Pandanus* leaf axils where the micro-environment remains moist). Rapid attainment of sexual maturity and short adult lifespan has been demonstrated for several other small-bodied tropical frogs (e.g. Barbault 1984, Rödel et al. 2004). However, only a few studies of tropical species have reported the percentage of the population that is sexually mature. These estimates range from 14 to 47% (Inger & Greenberg 1966, Brown & Alcala 1970, Stewart & Pough 1983), further confirming the short life span in *G. bicalcaratus* and *G. punctatus*.

Density and recruitment

Other studies that have quantified frog densities in the terrestrial environment have reported densities ranging from 0.00029/m² (*Syrrhophus marnocki*; Jameson 1955) to 5.92/m² (*Nectophrynoides occidentalis*; Lamotte 1959). While many factors can influence vari-

Microhabitat use and coexistence

These two closely-related species breed synchronously, and are both sympatric and syntopic throughout much of their range (Blommers-Schlösser & Blanc 1991). At the Sainte Luce forest, *Guibemantis bicalcaratus* and *G. punctatus* are often found in the same plants together and experiments have shown that competition between these two species is asymmetric (with *G. punctatus* being the superior larval competitor; Lehtinen 2005). Classic ecological theory predicts that if two species compete for a shared resource in a stable environment, one species will inevitably be driven to extinction (Gause 1934). My microhabitat use data suggest that the coexistence of *G. bicalcaratus* and *G. punctatus* at Sainte Luce may be facilitated, in part, by microhabitat niche partitioning within plants. These microhabitat differences, with *G. punctatus* found more frequently in wetter leaf axils than *G. bicalcaratus* (Fig. 5), may help reduce interspecific competition. At other sites in the eastern rainforest belt of Madagascar,

four or more species of *Pandanus*-breeding *Guibemantis* can be found. What factors facilitate the local coexistence of these species remains to be studied.

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Appendix
Early embryonic and larval development of
Guibemantis punctatus

A clutch of 28 eggs attended by a female was collected on 9 February 2001. The egg mass (including jelly) measured 46 mm × 43 mm at its widest points and was less than 24 hours old. Eggs were reared and development observed at ambient temperature (average ~ 27 °C) in an open-air field laboratory. Water was dripped over egg mass periodically to simulate rainfall. Observations recorded every 12 hours with 10 × hand lens. Stages are from GOSNER (1960).

Day 1 Late cleavage – animal pole gray, vegetal pole, white (stage 9)

Day 2 Most eggs are in late gastrula (stage 12) or early stage 13 (development of neural plate).

Day 3 Embryo elongated around remaining yolk. Tail is forming and head is distinctly larger than rest of the body. Occasional muscular response (Stage 17).

Day 4 Embryo 3.5 mm TL, tail very long. No noticeable heartbeat, but eye spots visible. Muscular response if disturbed (Stage 18).

Day 5 Heartbeat conspicuous. Continued elongation, tail fins apparent. Cornea not transparent, mouth not open. TL = 5 mm (Stage 20).

Day 6 Dark mottling now obvious on tail and venter. Yolk still fills gut. Jelly mass has now shrunk to 29 mm × 25 mm, and several hatchlings have wriggled down into the water. Hatchlings in the water are capable of uncoordinated swimming but mostly stay motionless on the bottom.

Day 7 All hatchlings now fully washed into the water. Most remain on bottom of container, but several cling to the sides with the head pointed upwards. Cornea transparent. Yolk fills abdominal cavity from posterior edge of heart to the vent. Mouthparts not obvious (Stage 21).

Day 8 Swimming now coordinated, but mouthparts not visible. Yolk still occupies entire abdominal cavity.

Day 9 All body surfaces covered with prominent dark spots. Mouthparts just beginning to form. Yolk still occupies gut but is noticeably smaller. On occasion, larvae are seen with their tails angled upwards at about 30° (TL = 7 mm).

Day 10 Mouthparts obvious, beginning differentiation. Yolk reduced in size, tail now heavily mottled with dark spots (Stage 23).

Day 11 Yolk now coiling into intestinal shape. Tail very dark, almost black.

Day 12 Yolk completely gone, replaced by a dark intestinal coil (TL = 8 mm, Stage 25).

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