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Rapid assessments of population sizes in ten species of Malagasy poison frogs, genus *Mantella*

ABSTRACT

Among the amphibians of Madagascar, the Malagasy poison frogs of the genus *Mantella* are the group that is most heavily collected for the pet trade. Although the taxonomy and genetic diversity of these frogs has been intensively studied in the past, very few data on their population dynamics are available, although such data are badly needed to evaluate and regulate their commercial collecting and export. Here we summarize available population density data on Malagasy poison frogs and report on own data based on rapid mark-recapture population estimates of ten *Mantella* species, carried out between 2003-2007. Population sizes usually were around 50-200 individuals, but these data must be seen as preliminary because they refer to specimens at particular reproduction sites (in swamps or along streams), and in some cases are heavily biased towards males since females were more difficult to collect. These partly very high population densities in our and previous studies refer to specimens gathering in very small areas (down to 50 square meters in *Mantella viridis* where the highest densities were recorded) and therefore can by no means be extrapolated to the whole distribution areas of these species. Long-term studies of the dynamics of particular populations, home ranges and dispersal, and of longevity and recruitment, need to be combined with such short-term density estimates to understand the perspectives of sustainable harvesting of Malagasy poison frogs.

Key words: Amphibians, Conservation, Madagascar, *Mantella,* Population estimate.

INTRODUCTION

Madagascar, because of its unique biodiversity, can be considered as a real living laboratory for biologists, deserving the highest priority for conservation

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(Myers et al., 2000). All currently described 238 species of non-introduced Malagasy amphibians are fully endemic on this fourth largest island of the world, and are not safe from a variety of threats (Andreone & Luiselli, 2003; Andreone et al., 2005). Despite a high intensity of recent research, Madagascar's amphibian diversity still has not revealed all its mysteries. Every year, researchers in Madagascar discover numerous undescribed species, and no full species inventory will be available in the next few years (Vences & Glaw, 2003). In addition, taxonomic revisions at the genus level have proven to be necessary after introduction of new methods, such as DNA analyses (Glaw & Vences, 2006).

The endemic Malagasy genus *Mantella* is currently constituted by 17 species (Vences et al., 1999). The systematics of the group is subject to revision using molecular techniques, which revealed that even within one species, considerable color variations can occur: this case was evidenced by mitochondrial DNA sequence analysis of different populations of *Mantella crocea* (variation of yellow to green), *Mantella milotympanum* (variation of red to green), and *Mantella baroni* (variation of extent of yellow dorsal colour), collected in different areas of Madagascar (Chiari et al., 2004, 2005; Rabemananjara et al., 2007a). The existence of different species groups in the genus has been first evidenced by allozyme analyses (Vences & Kniel, 1998), but until now, full taxonomic stability has not been reached. For example the brown species of *Mantella* in the *M. betsileo* complex are to be divided into various distinct lineages, at least one of which probably represents an undescribed species (Rabemananjara et al., 2007b). Besides major efforts in molecular systematics, a second line of research has, in the past years, focused on the alkaloid components of the skin of these frogs (Daly et al., 1996, 2002), and the biological origin of these toxins that are uptaken from the frog's prey (e.g., Daly et al., 1997; Clark et al., 2005).

Because of their attractive and variable pattern, almost all *Mantella* species are exploited for the international wildlife trade, this genus being the one with more exports in terms of Malagasy amphibians present in the pet trade (>230,000 individuals over 10 years 1994–2003) (Rabemananjara et al., *in press*). All representatives of the genus are actually included in appendix II of the Convention on the International Trade in Endangered Species (CITES) (Nairobi, Kenya, 10-20 April 2000). Madagascar ratified this convention in 1975 (ordinance 75-014 of 5 August 1975) to better protect and control the trade of living animals exported from the island. The Malagasy scientific authority is depending on thorough research results to set up the quotas of *Mantella* species, especially regarding population densities and species distributions which have remained largely unexplored.

Population density studies are difficult to perform in the tropics, because they are resource-intensive (Bailey et al., 2004), especially if carried out in remote areas that are often only reachable after hours of walking. An opportunity for such studies arose as in 2003 when a major project on the biology and alkaloid content of *Mantella* populations was started by the University of Antananarivo. During the fieldwork related to this study, populations of most *Mantella* species were visited and several rapid assessments of population densities obtained. In some cases, these data were already been made available to local authorities in the context of conservation management, but so far most data remained unpublished.

The present paper reviews all data available to us, published and unpublished, on density estimates of *Mantella* species, also adding new surveys that were carried out with similar methodology in the framework of other research projects. Our results refer to ten species of *Mantella* Boulenger, 1882, including *Mantella aurantiaca* Mocquard, 1900, *M. baroni* Boulenger, 1888, *M. bernhardi* Vences, Glaw, Peyrieras, Böhme & Busse, 1994, *M. betsileo* (Grandidier, 1872), *M. crocea* Pintak & Böhme, 1990, *M. laevigata* Methuen & Hewitt, 1913, *M. madagascariensis* (Grandidier, 1872), *M. milotympanum* Staniszewski, 1996, *M. pulchra* Parker, 1925 and *M. viridis* Pintak & Böhme, 1988. Four additional species, *M. cowani* Boulenger, 1882, *M. expectata* Busse & Böhme, 1992, *M. haraldmeieri* Busse, 1981 and *M. nigricans* Guibé, 1978, were also studied, but sample sizes were too low to obtain adequate mark-recapture estimates of population sizes. As we will emphasize again in the conclusions, the data presented here are far from thorough estimate of populations of *Mantella*, but they give the first and so far most reliable data of the approximate dimension of breeding aggregations of these frogs, across a wide array of species.

MATERIAL AND METHODS

Sites and study periods

Data were gathered over three survey periods per population within one reproductive cycle between June 2003 and April 2004. Some other independent studies were carried out between 2004 and 2007 by different researchers and are included in this manuscript (e.g., Vieites et al., 2005).

The study periods could roughly be classified according to four seasons: pre-reproduction (between September and November), reproduction (between December and February), post-reproduction (between March and April), and hibernation (between May and August). Most of the mark-recaptures took place during the breeding season (December-February) and in several of them (e.g., *M. baroni*, especially in the case of Kidonavo) the captured specimens were mostly males. In addition, the selected areas for the estimates were sites with high prevalence of *Mantella*, species which in general are known to be not continuously distributed but to aggregate at specific places (Daly et al., 1996). Hence, all density estimates for these frogs (previously published and herein) need to be taken with extreme caution as they only refer to particular sites, and the estimates in total numbers must be seen as minimum estimates (rapid assessments) that only refer to the part of the population that was gathering in the mating area at that particular time, and sometimes only to the males. In addition, several species occur along streams, like *M. baroni*, and specimens were collected along a linear transect following the stream which makes it even more difficult to relate population size estimates to a particular area.

Mark-recapture method

Mark-recapture is considered to be an adequate method to estimate population sizes and densities of amphibians (Funk et al., 2003; Bailey et al., 2004). Our surveys were carried out over short periods (2 days minimum and 7 days maximum) with 4 to 7 capture occasions. Considering that no concerted long-distance migrations of *Mantella* have been reported so far, and considering the periods between recaptures were fairly short (1.5 h to 24 h), we assumed that the studied populations were closed (see White et al., 1982). Toe-clipping of one toe was chosen for marking, considering that this technique allows high survival rates (>98%) (Hott & Scott David, 1999) and insures full mark retention, assumptions needed for mark-recapture methods (White et al., 1982). The capture effort was constant in most estimates, with 4 hour-persons (4 persons searching during one hour) per capture event, and recapture rates were up to 10% of previously marked individuals. The release of animals was carried out by each researcher in the plot section where they had been initially captured, to ensure the animals were spread enough over the whole study area and could mix with the rest of the population in a relatively short period. Due to the limited time available at each site it was not possible to apply individual markings to each specimen, and therefore the use of calculation methods available for open populations (such as the Jolly-Seber method) was not possible. We here apply the calculation method of Schnabel (1938) with 95% confidence intervals.

Population size estimates and summary of literature

The population size estimates from our data are summarized in Tab. I and range from 35 to 467 individuals. The original data used to calculate these values are reported in the Appendix. The confidence intervals were not very wide, and minimum and maximum population sizes ranged from 27-683 when confidence intervals were taken into account. From a total of 25 separate population estimates, 12 yielded population sizes below 100 individuals, and 17 yielded values below 200 individuals. Population estimates were highly variable among species, indicating that local conditions exert strong influences on the number of specimens gathering in a particular area for breeding. A slight indication is found that in species of the *Mantella betsileo* group (i.e., in *M. betsileo* and *M. viridis*), population sizes are on average larger than in others species: 4 out of 6 estimates were higher than 200 individuals, and the two highest values, above 400 individuals, corresponded to *M. viridis.* Since the populations of these two species studied here occur in rather dry, seasonal areas, the results may indicate that in these areas, the specimens aggregate even more strongly in a limited number of moist areas suitable for reproduction.

Data available so far, mostly from unpublished reports, always referred to population densities, not absolute numbers of individuals, and were as follows: For *Mantella aurantiaca*, Behra et al. (1995) observed densities between 14 to 230 individuals per hectare (ind/ha). For *M. bernhardi,* a density of 100-500 individuals by square km, thus 1 to 5 ind/ha, was mentioned for the

Species	Localities	Period	Population size N (Schnabel)	Population size with 95% c. i.	Study plot surface	"Density" /ha
Mantella aurantiaca	Andranomandry	21-23 Jan 2004	86	64 - 126	750m²	1267
	Torotorofotsy	20-25 Feb 2004	75	63 - 95	600m²	1317
	Torotorofotsy	21-22 Jan 2007	201	167 - 251	2500m²	836
Mantella baroni	Fanjavala	15-17 Jan 2004	108	81 - 161	2000m²	605
	Ampasimpotsy (Antoetra)	5-7 Dec 2003	92	78 -112	1089m²	872
	Kidonavo	21-29 Jan 2004	49	37 - 72	600m²	900
Mantella bernhardi	Mangevo, inside Ranomafana National Park	11-12 Dec 2003	41	32 - 59	750m²	600
	Mangevo, outside Ranomafana National Park	11-12 Dec 2003	316	254 - 420	750m²	4480
	Tolongoina	16-19 Dec 2003	73	57 - 101	750m²	1053
	Manombo	1-3 Feb 2004	88	60 - 163	480m²	2333
Mantella betsileo	Ankadirano	10-12 Sep 2003	253	207 - 325	400m²	6650
	Kirindy	27-29 Nov 2003	208	182 - 244	625m²	3392
Mantella crocea	Ankosy Marovoay	7-8 Feb 2004	35	27 - 49	200m²	1900
Mantella laevigata	Marojejy	20-21 Dec 2003	189	134 - 319	250m²	9040
		19-21 Mar 2004	154	97 - 378	250m²	9480
Mantella madagascariensis	Fanjavala	15-17 Jan 2004	186	132 - 314	2000m²	1115
Mantella milotympanum	Sahamarolambo (near Fierenana)	18-22 Feb 2003 (Vieites et al. 2005)	283*	---	6000 m²	470*
		11-13 Aug 2003	62	46 - 93	625m²	1120
		30 Jan - 1 Feb 2004	217	181 - 272	625m²	3616
		4-6 Apr 2004	86	69 - 111	625m²	1440
Mantella pulchra	An'Ala	9-11 Jan 2004	98	82 - 124	400m²	2575
Mantella viridis	Andranomantsina	30 Aug - 1 Sep 2003	467	407 - 548	50m²	95400
		26-28 Nov 2003	430	314 - 683	50m²	99600
	Andohatany	30 Aug - 1 Sep 2003	100	81 - 131	50m²	21200
		26-28 Nov 2003	75	49 - 157	50m²	20800

Tab. I. Summary of population size estimates carried out on *Mantella* populations using mark-recapture methods. The definitive densities were calculated based on population sizes averaged from the Schnabel estimator with 95% confidence interval. The population size of *M. milotympanum,* here reproduced from Vieites et al. (2005) (with asterisk) was calculated as average of Petersen (1896) estimates. Note the population "densities" calculated in the last column refer only to densities of the specimens at the study plots, and are merely reported to emphasize these frogs can occur in very dense breeding aggregations in very small areas, but these data should in no case be extrapolated to larger areas.

Ambohimanana zone, a site of intensive collecting using capture without release (Ramanamanjato et al., 1994). For *M. ebenaui,* densities between 100-253 ind/ha were reported in Zahamena during the reproductive period (Ramanamanjato et al., 1994). For this same species, in 1994, densities of 46 to 440 ind/ha and 100 ind/ha have been estimated respectively in Ankarana and Benavony (Rakotomavo, 2001), and in Lokobe, a density of 133-273 ind/ha in

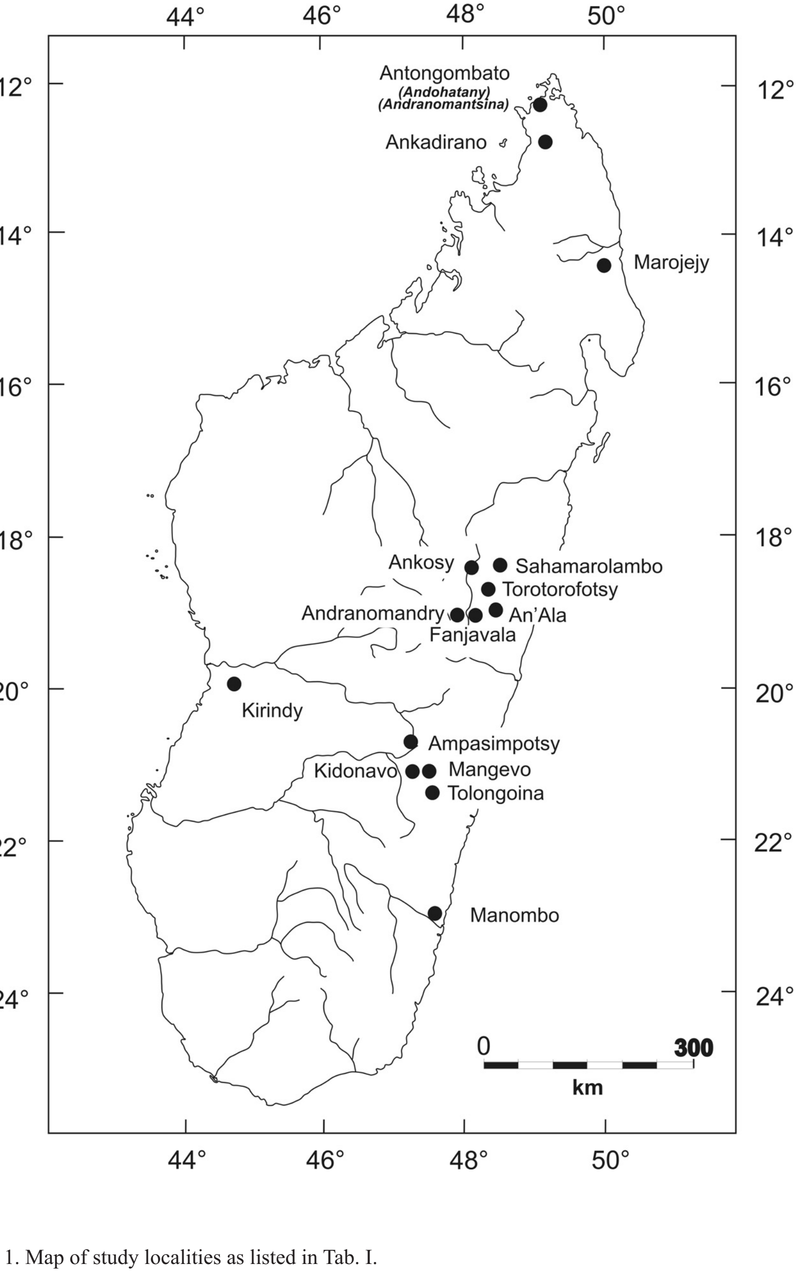

Fig. 1. Map of study localities as listed in Tab. I.

2000 (Rakotomavo, 2001). The methodology used for the estimates was not mentioned, and most of these estimates were reported under the name *M. betsileo* (but the north-eastern and north-western populations previously considered under that name are now assigned to *M. ebenaui;* see Rabemananjara et al., 2007b). For *M. cowani,* species for which we were unable to obtain population size data, the following density estimates in the Antoetra region in 1996, during the reproduction period, have been mentioned: 1050 ind/ha in the marshy area, 750 ind/ha in savannah, 350 ind/ha in eucalyptus forest, 750 ind/ha in edge and 550 ind/ha in bamboo forest, in Andalasakaviro, 110 ind/ha and 190 ind/ha in Amparihimazava (BIODEV ,1996). The methodology used was the cumulative capture without release. For *M. haraldmeieri,* a further species where we could not obtain appropriate sample sizes, 760 individuals per hectare were estimated in the low valley of Manantantely and 50 on the flank in January 1996 (BIODEV 1996). For *M. milotympanum*, earlier studies revealed densities of 1614-3000 ind/ha in March and 500-1652 ind/ha in May 1994 (Ramanamanjato et al., 1994); and 100-500 ind/ha in 2000 during hibernation (Rakotomavo, 2001). For *M. viridis,* at Montagne des Français, densities of 88-492 were observed in August 1994, and 15-242 ind/ha in February 1996 (BIODEV, 1996; Ramanamanjato et al., 1994).

Despite the qualifications applying to the calculation of densities of these frogs per surface area (see Materials and Methods), which clearly is highly dependent on the definition of the study plot, we here calculated “densities” for our populations, in order to be able to compare them with the information available so far in unpublished reports, summarized in the previous paragraph. Except for one estimate of *M. milotympanum* of 3000 ind/ha (Ramanamanjato et al., 1994), all of the estimates obtained previously were below or around 1000 ind/ha. In contrast, most of our data are clearly higher than 1000 ind/ha, and several were distinctly higher than that. Previous estimates, as far as known, usually applied capture without release or transect counting, and were usually also carried out in favourable areas were *Mantella* individuals gathered for reproduction. This indicates that mark-recapture will probably give higher and probably more realistic estimates of population sizes of *Mantella* although long-term methodological comparisons are not available so far.

CONCLUSIONS

According to the data presented herein, it appears that *Mantella* usually gather in areas suitable for reproduction in populations of about 50-200 individuals at a particular moment. However, the actual populations are much larger, since many individuals will be far from the reproduction area at the particular time of survey, especially females after egg deposition and juveniles which were very rarely found in our surveys. It is remarkable that despite the methodological constraints of our short-term mark-recapture studies, the estimated population sizes are quite similar for all species. The “densities” show much stronger differences among species, sites and seasons. This can be explained by the fact that sometimes reproductive sites can be small areas where all specimens concentrate (especially in species from dry regions, as *M. viridis* and *M. betsileo*), whereas in other cases breeding sites can be more evenly spaced. Under such conditions, defining the study plot area will have enormous effects for any spatial analysis of the population size data.

Our data provide important baseline data for conserving *Mantella* frogs and corroborate further indications (e.g., Vences et al., 2004; Vieites et al., 2005) that, for many species in this genus, population sizes in heavily exploited areas are not necessarily lower than in pristine areas without commercial collecting activity (e.g., *Mantella madagascariensis, M. milotympanum, M. aurantiaca*). However, without long-term and more detailed studies on population structure and dynamics of these frogs, our data are insufficient to quantitatively assess strategies for sustainable harvesting of these species.

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RÉSUMÉ

Estimation rapide de la grandeur taille de population en dix espèces de grenouilles poison de Madagascar, gendre Mantella.

De rapides évaluations des dimensions de population de dix espèces de grenouilles poison, le genre *Mantella*, montrent qu'il s'agit du groupe le plus massivement collecté par le marché des animaux de compagnie. Bien que la taxonomie et la diversité génétique de ces grenouilles ait été intensément étudié dans le passé, très peu de données sur sa dynamique de population sont disponibles, quoique de telles données soient mauvaises pour évaluer et réguler leur collecte commerciale et leur exportation. Ici nous résumons des données disponibles sur la densité de population de grenouilles poison malgaches et référençons chaque donnée estimée à partir de balises sur dix espèces de *Mantella*, accomplis entre 2003 et 2007. Les dimensions de la population se situaient généralement autour de 50 à 200 individus, mais ces données doivent être seulement prises comme préliminaires car elles se réfèrent à des spécimens pris sur des sites particuliers de reproduction (dans des marais ou le long de cours d'eau), et dans certains cas sont fortement partiales envers les males puisque les femelles sont beaucoup plus difficile à collecter. Une partie de ces densités de populations très élevées dans nos études et celles qui sont prévues se réfère à des spécimens ramassés dans de très petites aires (inférieures à 50 mètres carrés où les plus hautes densités ont été enregistrées) et ne peut donc pas être extrapolée à l'ensemble des zones de distribution de ces espèces. Des études sur le long terme sur les dynamiques de populations particulières, ainsi que sur la longévité et la collecte, doivent être combinées avec des études sur le court terme d'estimations de densité, pour comprendre les perspectives de la récolte pérenne des grenouilles poison Malgaches.

Mots clés: Amphibiens, Conservation, Madagascar, *Mantella*, Population éstimée.

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APPENDIX: SUMMARY OF THE ORIGINAL MARK-RECAPTURE DATA USED FOR ESTIMATION OF POPULATION SIZES.

Data for each species and localitiy are presented as N/r/m for each capture occasion, where N is the total number of specimens captured on that capture occasion, r is the number of recaptured specimens on that capture occasion, and m is the number of marked specimens in the population before that particular capture occasion. At the end of each mark-recapture series we give the number of total marked specimens in the population at the end of the experiment, which can be seen as the minimum population size.

M. aurantiaca - Andranomandry 21-23 Jan 2004: 24/0/0, 20/13/24, 25/8/31, 15/6/48, 21/10/57, **68.** *M. aurantiaca* - Torotorofotsy 20-25 Feb 2004: 26/0/0, 24/15/26, 38/18/35, 45/26/55, 34/33/74, **75.** *M. aurantiaca* - Torotorofotsy 21-22 Jan 2007: 50/0/0, 46/17/50, 59/13/79, 51/30/125, 38/34/146, **150.** *M. baroni* - Fanjavala 15-17 Jan 2004: 18/0/0, 10/2/18, 25/5/26, 36/14/46, 19/14/68, **73.** *M. baroni* - Ampasimpotsy Antoetra 5-7 Dec 2003: 38/0/0, 49/18/38, 52/42/69, 37/33/79, 33/28/83, **88.** *M. baroni* - Kidonavo 21-29 Jan 2004: 8/0/0, 9/3/8, 13/6/14, 9/3/21, 10/3/27, 13/12/34, 5/3/35, 5/4/37, 9/4/38, **43.** *M. bernhardi* - Mangevo, inside Ranomafana National Park 11-12 Dec 2003: 16 0 0, 17 4 16, 10 7 29, 22 19 32, 16 14 35, **37.** *M. bernhardi* - Mangevo, outside Ranomafana National Park 11-12 Dec 2003: 20/0/0, 38/0/20, 104/16/58, 90/47/146, **189.** *M. bernhardi* - Tolongoina 16-19 Dec 2003: 22/0/0, 30/9/22, 22/16/43, 21/10/49, 17/15/60, **62.** *M. bernhardi* - Manombo 1-3 Feb 2004: 5/0/0, 21/2/5, 19/5/24, 27/11/38, **54.** *M. betsileo* - Ankadirano 10-12 Sep 2003: 45/0/0, 67/9/45, 27/12/103, 52/28/118, 55/29/142, **168.** *M. betsileo* - Kirindy 27-29 Nov 2003: 49/0/0, 91/28/49, 80/29/112, 70/60/163, 72/62/173, **183.** *M. crocea* - Ankosy 7-08 Feb 2004: 21/0/0, 23/16/21, 22/16/28, 16/15/34, **35.** *M. laevigata* - Marojejy 20-21 Dec 2003: 12/0/0, 12/0/12, 26/2/24, 25/7/48, 36/14/66, **88.** *M. laevigata* - Marojejy 19-21 Mar 2004: 17/0/0, 13/2/17, 12/2/28, 13/1/39, 13/6/51, **57.** *M. madagascariensis* - Fanjavala 15-17 Jan 2004: 38/0/0, 26/5/38, 13/4/59, 17/5/68, 17/9/80, **88.** *M. milotympanum* - Sahamarolambo (Fierenana) 11-13 Aug 2003: 14/0/0, 17/4/14, 22/8/27, 31/22/41, **50.** *M. milotympanum* - Sahamarolambo (Fierenana) 30 Jan-01 Feb 2004: 57/0/0, 68/18/57, 43/27/107, 31/12/123, 59/38/142, **163.** *M. milotympanum* - Sahamarolambo (Fierenana) 4-6 Apr 2004: 25/0/0, 32/12/25, 38/26/45, 31/19/57, 30/17/69, **82.** *M. pulchra* - An'Ala 09-11 Jan 2004: 20/0/0, 43/13/20, 42/24/50, 42/31/68, 41/24/79, **96.** *M. viridis* - Andranomantsina 30 Aug - 1 Sep 2003: 56/0/0, 78/17/56, 127/40/117, 79/40/204, 193/79/243, **347.** *M. viridis* Andohatany 30 Aug - 1 Sep 2003: 27/0/0, 46/10/27, 37/25/63, 43/33/75, **85.** *M. viridis* Andranomantsina 26-28 Nov 2003: 41/0/0, 36/7/41, 43/5/70, 34/8/108, 29/8/134, **155.** *M. viridis* Andohatany 26-28 Nov 2003: 21/0/0, 10/4/21, 12/4/27, 10/3/35, 4/3/42, **43.**