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Stomach content analyses in Malagasy frogs of the genera *Tomopterna, Aglyptodactylus, Boophis*, and *Mantidactylus* (Anura: Ranidae)

Mageninhaltsanalysen bei madagassischen Fröschen der Gattungen *Tomopterna, Aglyptodactylus, Boophis* und *Mantidactylus* (Anura: Ranidae)

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KURZFASSUNG

Mageninhaltsanalysen an 228 konservierten Exemplaren der madagassischen Raniden *Tomopterna labrosa, Aglyptodactylus madagascariensis, Boophis laurenti, B. tephraeomystax, Mantidactylus liber, M. granulatus, M. cornutus, M. redimitus, M.* cf. *leucomaculatus, M. boulengeri, M.* cf. *asper, M. luteus, M. ulcerosus, M. betsileanus, M. femoralis, M. lugubris, M.* cf. *lugubris* und dem *M. albofrenatus* - Komplex erlaubten die Identifizierung von 417 Beutetieren. Dabei handelte es sich hauptsächlich um Insektenlarven (28,5%), Ameisen (18,2%), Käfer (14,9%), orthopteroide Insekten (11,5%) und Spinnen (6,7%). Ameisen wurden bei den meisten Arten in Anteilen von 0% bis 48% gefunden, nur bei *M. liber* wurde ein höherer Prozentsatz (68%) nachgewiesen. In drei Fällen fanden sich Wirbeltiere als Nahrung (zwei Frösche und ein frisch geschlüpftes Chamäleon). Spektrum und Größe der Beutetiere variierten zwischen den meisten Arten nur wenig.

Viele der untersuchten Frösche (20 %) hatten leere Mägen. Für das gesamte Material lag die mittlere Anzahl von Beutetieren pro Exemplar bei 1,8; im artlichen Vergleich war sie bei *M. lugubris* mit durchschnittlich 5,4 am größten. Die höchste Anzahl von Beutetieren, die in einem Frosch (*M. albofrenatus* - Komplex) gefunden wurde, lag bei 34. Die meisten nachgewiesenen Beutetiere hatten Längen zwischen 4 und 5 mm. Die größten Beutetiere maßen zwischen 30 und 40 mm. Bei allen Froscharten außer *A. madagascariensis* und *M. liber* konnten Beutetiere mit Längen über 10 mm gefunden werden.

Diese Ergebnisse werden im Kontext unterschiedlicher Beutefangstrategien diskutiert (Lauerjäger gegenüber aktiven Beutesuchern, Ameisenspezialisten gegenüber Generalisten). Bei den untersuchten Arten handelt es sich vermutlich eher um Generalisten. Die erhobenen Daten über *Mantidactylus* werden mit denen von *Mantella* verglichen, die eine mikrophage und myrmecophage Ernährungsspezialisierung aufweist. Die Tatsache, daß *Mantidactylus liber* kleinere Beute und einen höheren Prozentsatz an Ameisen zu fressen scheint als andere *Mantidactylus*-Arten, stellt einen weiteren Hinweis auf die vermuteten engen verwandtschaftlichen Beziehungen dieser und nahe verwandter Arten zur Gattung *Mantella* dar.

ABSTRACT

417 prey items were identified in the stomach contents of 228 preserved specimens of the Malagasy ranid frog species *Tomopterna labrosa, Aglyptodactylus madagascariensis, Boophis laurenti, B. tephraeomystax, Mantidactylus liber, M. granulatus, M. cornutus, M. redimitus, M.* cf. *leucomaculatus, M. boulengeri, M.* cf. *asper, M. luteus, M. ulcerosus, M. betsileanus, M. femoralis, M. lugubris, M.* cf. *lugubris*, and the *M. albofrenatus* complex. These mainly were insect larvae (28.5%), ants (18.2%), beetles (14.9%), orthopteroid insects (11.5%), and spiders (6.7%). Ants were eaten by most species in rates of 0% to 48%, while a higher percentage (68%) was noted in *M. liber*. In three cases, vertebrate prey was recorded (two frogs and one chameleon hatchling). Prey sizes and prey types consumed differed but slightly between most species.

20 % of the specimens examined had empty stomachs. Mean number of prey items over all frog specimens was 1.8; comparing taxa, the maximum mean number of 5.4 was found in *M. lugubris*. The largest number of prey items found in one specimen (*M. albofrenatus* complex) was 34. The lengths of most prey items consumed varied between 2 and 20 mm, with an overall modal value between 4 and 5 mm. The largest prey items consumed had lengths between 30 and 40 mm. In all species, items larger than 10 mm were found, except in *A. madagascariensis* and *M. liber*.

The results are discussed in the context of different feeding strategies (sit and wait predators versus active foragers; ant specialists versus generalists). The species examined probably are generalized feeders. The data on *Mantidactylus* species is compared with that of *Mantella* species, which are known to be microphagous and myrmecophagous specialists. The fact that *Mantidactylus liber* seems to consume smaller prey and a higher percentage of ants than other *Mantidactylus* of similar size may further support the assumption of its close phylogenetic relationships to *Mantella*.

KEY WORDS

Amphibia: Anura: Ranidae; Madagascar; food; feeding strategies; *Tomopterna labrosa, Aglyptodactylus madagascariensis, Boophis laurenti, B. tephraeomystax, Mantidactylus liber, M. granulatus, M. cornutus, M. redimitus, M.* cf. *leucomaculatus, M. boulengeri, M.* cf. *asper, M. luteus, M. ulcerosus, M. betsileanus, M. femoralis, M. lugubris, M.* cf. *lugubris, M. albofrenatus* complex

INTRODUCTION

Although anurans generally are considered to be feeding generalists, some species have been demonstrated to be selective in their feeding (DUELLMAN & TRUEB 1986). Remarkable feeding specializations are those of the aquatic, tongueless Pipidae which transport the food into the mouth through water currents produced by hyobranchial pumping movements (SOKOL 1969), large, macrophagous species such as the South African species *Pyxicephalus adspersus* TSCHUDI, 1838, the snail-eating species of the hyperoliid genus *Paracassina* (DREWES & ROTH 1981), and the burrowing *Rhinophrynus dorsalis* DUMÉRIL & BIBRON, 1841 which projects its tongue by hydrostatic pressure (TRUEB & GANS 1983). Recent evidence indicates that beside these exceptional examples, feeding specializations are common even among frog groups which were thought to be more generalized in this respect. Some dendrobatid genera seem to be specialized in microphagous and myrmecophagous feeding in different degrees, presumably reflecting their phylogenetic relationships (TOFT 1995; CALDWELL 1996). A similar myrmecophagous feeding is found in other alkaloid containing anurans (VENCES & al. 1998; VENCES & KNIEL 1998), and is probably common among microhylid, leptodactylid and myobatrachid frogs (DONNELLY 1991; VENCES pers. obs.). Feeding specializations are often reflected by modified skull and tongue shape (EMERSON 1985; HORTON 1982; VENCES & al. 1998), and their identification is therefore important for the recognition of the adaptive nature of character complexes which are frequently used uncritically in phylogenetic studies.

Some data on the food of Malagasy anurans has been published by BLOMMERS-SCHLÖSSER (1975), referring to stomach contents of several microhylids, and by VENCES & KNIEL (1998) on the mantelline genus *Mantella*. Only some cursorial data is available on the stomach contents of the second mantelline genus *Mantidactylus* (GLAW & VENCES 1994), the rhacophorine genus *Boophis* (GLAW & VENCES 1997), and the ranine genus *Aglyptodactylus* (GLAW & al. 1998), whereas nothing was published on the food of the Malagasy frogs of the ranine genus *Tomopterna*.

The aim of the present paper is to provide for the first time quantitative data on the food spectrum of representatives of these four genera, based on stomach content analyses of preserved specimens. Since the studied material was collected at different localities and different times, we are not able to present data about niche partitioning (as e.g. TOFT 1980a, b, 1985), seasonal prey variation (as e.g. DONNELLY 1991), or differential prey selection.

MATERIALS AND METHODS

We studied a total of 228 specimens of the collection of the Museum National d'Histoire Naturelle, Paris (MNHN). The specimens were dissected by a longitudinal cut on the venter; stomachs and intestines were removed and opened, and their contents were examined under a stereo microscope by one of the authors (C. Z.) Snout-vent length (SVL) to the nearest mm was recorded for each frog specimen using callipers. Prey items were counted, classified down to higher taxonomic groups, and measured for their total length. The identified prey items were attributed to one of the following taxonomic categories (in parentheses: a more detailed assignment of the prey items found): (1) Crustacea (isopods, crabs), (2) Myriapoda (millipedes), (3) Araneae (spiders), (4) Apterygota (collembola and thysanurans), (5) orthopteroids, including Dermaptera, Blattodea, Saltatoria, and Isoptera (most frequently recorded items were Saltatoria), (6) Hemiptera (cicadas and bugs), (7) Hymenoptera: Formicidae (ants, including winged specimens), (8) Hymenoptera others than ants, (9) Diptera, (10) Coleoptera, (11) insect larvae, (12) undetermined insects or insect remains, (13) others. In some cases of fragmentary prey items, we estimated original total length from the preserved remains (e. g., hindlegs of Saltatoria, elytrae of Coleoptera, heads of ants).

Percentages given indicate relative numbers of prey items.

Most of the anuran specimens examined had been collected during the 1970s by French expeditions; detailed collecting dates were not available from the MNHN catalogues. Species examined and localities of the specimens (according to the MNHN catalogue), were as follows:

Tomopterna labrosa COPE, 1868: MNHN 1973.464 (Ambatoandrano), 1895.248A, 246, 1953. 199, 201;

Aglyptodactylus madagascariensis (DUMÉRIL, 1853): MNHN 1975. 202, 204 (Ranomafana), 212, 227 (Moramanga-Niagarakely), 240, 254, 256, 262 (Perinet), 270 (Ambana), 271 (Ambala-Manakara), 288 (Ambalamarovandana 1530 m);

Boophis tephraeomystax (DUMÉRIL, 1853): MNHN 1975.2517 (Maroantsetra), 2525, 2529 (Mahanoro), 2530 (Mananara), and six specimens without locality (2542, 2543, 2550, 2555, 2567, 2578);

Boophis laurenti GUIBÉ, 1947: MNHN 1972.241 (Andringitra; Ibory, pied nord), 287 (Andringitra; Andohariana), 338, 365 (Andringitra; Ampiadianombilahy), 357, 377 (Andringitra; Pic Boby), 358, 382 (Andringitra; Cuvette Boby), 396 (Andringitra; Andohabatomena);

Mantidactylus liber (PERACCA, 1893): MNHN 1972. 1254-1255 (Ambohitantely), 1973.973, 976, 1029, 1030, 1035 (Marojezy 1300 m), 1026 (Sambava, forêt costiere), 1975.798 (Itampolo), 802 (Ambatoandrano);

Mantidactylus boulengeri METHUEN, 1919: MNHN 1991.3153, 3156, 1972.1878-1880, 1930, 1937, 1940-1941, 1958, 1981-1983, 1986, 2032, 2041, 2046, 2053 (all from Chaines Anosyennes);

Mantidactylus luteus METHUEN & HEWITT, 1913: MNHN 1972. 1405, 1410 (Camp V, Chaines Anosyennes), 1973.901 (Marojezy, 300 m);

Mantidactylus cf. *asper* (BOULENGER, 1882): MNHN 1893.243, 248, 1972.573 (M. d'Ambre), 1975.322, 324-325, 329-31 (Les Rousettes), 326 (Ifaty), 327 (Antsalova, Antsingy), 332 (sans origine precise);

Mantidactylus granulatus (BOETTGER, 1881): MNHN 1973.914 (Marojezy 300 m), 931 (Marojezy 1300 m);

Mantidactylus cornutus (GLAW & VENCES, 1992): MNHN 1972.1471-1472 (Chaines Anosyennes), 1973.912 (determination uncertain) (Marojezy, 1300 m), 1991. 2940;

Mantidactylus cf. *leucomaculatus* (GUIBÉ, 1975): MNHN 1973.928 (Marojezy 600 m), 1973. 922, 924, 926, 929, 933 (Marojezy 1300 m);

Mantidactylus redimitus (BOULENGER, 1889): MNHN 1973.911 (Marojezy 600-1300 m), 937 (Marojezy 300 m), 938, 940-941 (Marojezy 600 m);

Mantidactylus ulcerosus (BOETTGER, 1880): MNHN 1893.224, 227, 230-231 (Mararaomby), 256 (Ambre, Mararaomby), 1962.870 (Ambre), 873, 875 (Nosy Be), 632 (Bas Manongarivo), 670 (Ambilobe);

Mantidactylus betsileanus (BOULENGER, 1882): MNHN 1972.1486, 1488, 1492, 1494 (Ambana), 1495 (Chaines Anosyennes, Camp IV et III bis), 1499 (Chaines Anosyennes, Camp IV), 1973.768, 793 (Marojezy 300 m), 1973.789 (Marojezy 1300 m);

Mantidactylus femoralis (BOULENGER, 1882): MNHN 1973.833, 835 (Ambatomenaloha, Itremo), 836, 846 (Ambatomenaloha), 849 (Andringitra, Ambatomenaloha), 853 (Marojezy 1300 m, sommet), 864, 865 (Marojezy 1300 m), 873, 874 (Marojezy 600 m);

Mantidactylus cf. *lugubris* (DUMÉRIL, 1853): MNHN 1973.882, 884-885, 887-91, 893 (all Marojezy, 300 m except 1973.882: Marojezy, 1300 m);

Mantidactylus lugubris (DUMÉRIL, 1853): MNHN 1972.1577, 1584-1585, 1595, 1675 (all Chaines Anosyennes, Camp IV);

Mantidactylus albofrenatus (MÜLLER, 1892) complex: MNHN 1930.411-412, 415, 1935.154-158, 1946.362, 1953.98-101, 1972.536 (Col Ivohibe, forêt Marovitsika), 1972.537 (Moramanga), 1972.538-46 (Col Ivohibe, forêt Marovitsika), 547-548 (Soavala), 549 (Ambohitantely), 550 (Soavala-Camp I), 1972.1328 (Bekazaha), 1329 (Vallee Mahiavona, Ankaratra), 1330-43, (Chaines Anosyennes; Ambana-Soavala), 1344-1346, 1349-54 (Chaines Anosyennes; Camp IV et III bis), 1975.367-370, 374, 386, 388 (sans origine precise), 371-372, 377, 384, 385 (Marojezy 600 m), 373 (Ranomafana), 375 (Marojezy 1300 m), 376 (Perinet), 378, 387 (Marojezy 300 m) 379-381 (sans origine precise), 1975.382 (Ranomafana), 383 (Massif de l'Andohahela), 1989.3576-3583, 3585-3586.

The forms named *M.* cf. *leucomaculatus*, *M.* cf. *asper*, and *M.* cf. *lugubris* here are probably new, undescribed species. However, *M.* cf. *lugubris* which is characterized by a very short snout can not reliably be distinguished from *M. lugubris* at the current state of knowledge; both forms were therefore treated as one. The species *M. opiparis* (PERACCA, 1893) and *M. albofrenatus* (subgenus *Chonomantis*) as currently understood (see GLAW & VENCES 1994) actually comprise several additional species (GLAW pers. obs.). Specimens are here referred to as *M. albofrenatus* complex. Also the subgenus *Brygoomantis* (here included: *M. betsileanus* and *M. ulcerosus*) needs systematic revision.

RESULTS

Overall, we identified a total of 417 prey items. Of these, the largest portion were insect larvae (28.5%), followed by ants (18.2%), coleopterans (14.9%), orthopteroids (11.5%), spiders (6.7%), crustaceans (2.9%), and hemipterans (2.2%); 8.2% of the prey belonged to unidentified insects (table 1). The large percentage of insect larvae is rather surprising; however, a closer look shows that this is mainly

Table 1: Number of prey items identified in stomachs and intestines of studied species of *Tomopterna*, *Aglyptodactylus*, *Boophis*, and *Mantidactylus*, classified by taxonomic groups. # - presence of additional remains belonging to the corresponding taxonomic group but not assignable to individual prey items; Crust - Crustacea (isopods and crabs); Myria - Myriapoda (millipedes); Aran - Araneae (spiders); Apter - Apterygota (collemboles and thysanurans); Orthop - Orthopteroids (including Dermaptera, Blattodea, Saltatoria, and Isoptera); Hemip - Hemiptera (cicadas and bugs); Hymen Form - Hymenoptera: Formicidae (ants, including winged specimens); Hymen others - Hymenoptera others than ants; Dip - Diptera; Coleop - Coleoptera; Insecta indet - undetermined insects or insect remains. Shaded lines mark species with a small sample size (N < 7).

Tabelle 1: Anzahl der Beutetiere, die in Mägen und Darmtrakten der untersuchten Arten von *Tomopterna*, *Aglyptodactylus*, *Boophis* und *Mantidactylus* nachgewiesen wurden, geordnet nach taxonomischen Gruppen. # - Anwesenheit von weiteren Resten der entsprechenden Gruppe, die nicht individuellen Beutetieren zugeordnet werden konnten; Crust - Crustacea (Asseln und Krabben); Myria - Myriapoda (Tausendfüßer); Aran - Araneae (Spinnen); Apter - Apterygota (Springschwänze und Silberfischchen); Orthop - Orthopteroida (einschließlich Dermaptera, Blattodea, Saltatoria und Isoptera); Hemip - Hemiptera (Zikaden und Wanzen); Hymen Form - Hymenoptera: Formicidae (Ameisen, inklusive geflügelter Geschlechtstiere); Hymen others - Hymenoptera, andere als Ameisen; Dip - Diptera; Coleop - Coleoptera; Insecta indet - nicht näher bestimmte Insekten oder Insektenreste; Others - andere. Arten mit einer geringen Stichprobengröße (N < 7) sind grau hinterlegt.

Specimens examined / Untersuchte Exemplare	Crust	Myria	Aran	Apter	Orthop	Hemip	Hymen Form	Hymen others	Dip	Coleop	Insecta (larvae)	Insecta indet	Others	Total / Gesamt
T. labrosa	0	0	1	0	1	0	0	0	0	6	0	#	1 (frog)	9
A. madagascariensis	0	0	1	0	2#	1	3	0	0	7	2	1#	1 (embiopteran?)	18
B. tephraeomystax	0	0	0	0	#	0	0	0	1	2	2	0#	0	5
B. laurenti	0	0	1	0	0	1	0	0	0	1	1	0#	0	4
M. liber	0	0	0	0	0	0	13	0	0	2	2	2#	0	19
M. granulatus	0	0	0	0	0	0	0	0	0	1	0	0	0	1
M. cornutus	0	0	0	0	1#	0	0	0	0	0	0	3#	0	4
M. cf. *leucomaculatus*	0	0	1	0	1	0	0	0	0	3	3	3	0	11
M. redimitus	0	1	0	0	0	0	1	1	1	#	0	0#	0	4
M. boulengeri	5	0	2	0	20 (17 Isoptera)	2	16	0	1	6	9	5#	1 (pseudoscorpion)	67
M. luteus	0	0	0	0	0	0	0	0	0	1	0	#	0	1
M. cf. *asper*	1	0	2	0	1	0	1	0	1	1	1	4#	0	12
M. ulcerosus	0	0	2	0	3	0	0	0	0	0	0	0#	1 (frog)	6
M. betsileanus	0	0	2	0	0	2	1	4	0	2	4	0#	0	15
M. femoralis	2	0	7	0	5	1	4	0	1	14	4	5#	1 (chameleon)	44
M. lugubris/cf. *lugubris*	2	0	0	1	2	1	18	0	2	6	4	3#	0	39
M. albofrenatus complex	2	2	9	5	12#	1	19	2	0	9	87	9#	1 (neuropteran larva)	158
Total / Gesamt	12	3	28	6	48	9	76	7	7	62	119	36	6	417

Table 2: Number of prey items identified in stomachs and intestines of studied species of *Tomopterna*, *Aglyptodactylus*, *Boophis*, and *Mantidactylus*, classified according to their size (total length). Mean snout-vent length of the N frog specimens of each species is also given. Shaded lines mark species with a small sample size (N < 7).

Tabelle 2: Anzahl der Beutetiere, die in Mägen und Darmtrakten der untersuchten Arten von *Tomopterna*, *Aglyptodactylus*, *Boophis* und *Mantidactylus* nachgewiesen wurden, geordnet nach ihrer Größe (Gesamtlänge). Die Tabelle führt auch die mittlere Kopf-Rumpf-Länge (SVL) der N untersuchten Exemplare jeder Froschart auf. Arten mit einer geringen Stichprobengröße (N < 7) sind grau hinterlegt.

Specimens examined / Untersuchte Exemplare			Number of prey items in the size classes / Anzahl von Beutetieren in den Größenklassen								
Taxon	N (number of specimens) / (Anzahl Exemplare)	SVL (mean) Kopf-Rumpflänge	< 1 [mm]	1 [mm]	2 [mm]	3 [mm]	4-5 [mm]	6-10 [mm]	11-20 [mm]	>20 [mm]	Total / Gesamt
T. labrosa	5	62.4	0	0	0	2	1	3	2	1	9
A. madagascariensis	11	44.7	0	0	1	0	5	12	0	0	18
B. tephraeomystax	10	40.5	0	0	0	0	0	3	2	0	5
B. laurenti	9	39.0	0	0	0	0	1	2	1	0	4
M. liber	10	25.3	0	0	8	8	1	2	0	0	19
M. granulatus	2	39.0	0	0	0	1	0	0	0	0	1
M. cornutus	4	41.0	0	0	0	0	2	1	1	0	4
M. cf. *leucomaculatus*	6	35.5	0	0	0	1	1	8	1	0	11
M. redimitus	5	46.6	0	0	0	0	1	1	1	1	4
M. boulengeri	19	25.9	0	0	4	14	18	27	2	2	67
M. luteus	3	42.3	0	0	0	0	1	0	0	0	1
M. cf. *asper*	13	36.2	0	0	1	0	2	6	3	0	12
M. ulcerosus	10	38.7	0	0	0	0	1	2	2	1	6
M. betsileanus	10	37.0	0	0	0	1	3	6	5	0	15
M. femoralis	10	45.9	1	2	8	5	13	10	2	3	44
M. lugubris/cf. *lugubris*	14	30.3	0	1	3	16	14	4	0	1	39
M. albofrenatus complex	85	28.0	0	3	10	15	102	25	3	0	158
Total / Gesamt	226	33.4	1	6	35	63	166	112	25	9	417

caused by the large number of larvae eaten by two specimens of the *M. albofrenatus* complex. Stomachs of MNHN 1972.1345 (37 mm SVL) and MNHN 1972.1354 (28 mm SVL) collectively contained 62 insect larvae. Excluding the *M. albofrenatus* complex from the analysis, percentage of insect larvae over all species was 12.4% only, whereas ants (22%) and coleopterans (20.5%) accounted for the highest rates.

The highest percentages of ants were found in *M. lugubris* (48%) and *M.* cf. *lugubris* (42%), and especially in *M. liber* (68%); in the other species, percentages varied between 0 and 24%. Termites (here included under orthopteroids) were only found once, in a specimen of *M. boulengeri* (33 mm SVL, MNHN 1972.2046) which had consumed 7 ants and 17 termites. Mites, another prey class often consumed by anurans, were not found at all. Although single mites, which can be very small and difficult to identify, may have been overlooked, the examined anuran specimens certainly had not consumed this prey type in large numbers.

Presumably aquatic or semi-aquatic arthropods were found in two frog species known to be brook bank dwellers: *M. betsileanus* (MNHN 1973.789) contained a case-bearing trichopteran larva, and *M. lugubris* (MNHN 1972.1585) a small crab (4 mm).

Three of the examined specimens had eaten vertebrate prey. *M. femoralis* (42 mm SVL, MNHN 1973.835) had eaten a chameleon hatchling (genus *Calumma* or *Furcifer*, 40 mm in total length), whereas *M. ulcerosus* (33 mm SVL, MNHN 1962.875) and *T. labrosa* (54 mm SVL, MNHN 1973.464) had eaten a small frog each (9 mm and 25 mm SVL, respectively).

46 of the specimens examined (20 %) had empty stomachs. Another 35 specimens (15.4%) had only unidentifiable remains in their stomachs. In some cases, e. g. in the high-mountain species *B. laurenti*, this may have been caused by the collecting time, since in seasonal environments, feeding may be limited to certain periods. Mean number of prey items over all 228 specimens was 1.8, but also in species where stomachs were generally not empty, such as *M. boulengeri*, *M. lugubris*, and *M. femoralis*, mean prey number per frog was not very high (3.5, 5.4 and 4.4, respectively). The largest number of prey items was found in the above mentioned specimens of the *M. albofrenatus* complex (MNHN 1972.1345 and 1354; 34 and 31 items, respectively), and in *M. femoralis* (MNHN 1973.835; 24 items).

Most prey items consumed measured between 2 and 20 mm in length, with an overall modal value between 4 and 5 mm (table 2). Modal prey size class was 6-10 mm in most species, except for the *M. albofrenatus* complex and *M. femoralis* (4-5 mm), *M. lugubris* / *M.* cf. *lugubris* (3 mm), and *M. liber* (2-3 mm). In all species (those with sample size < 7 are not considered here), items longer than 10 mm were observed, except in *A. madagascariensis* and *M. liber*. The largest prey items consumed were, beside the chameleon (see above), insect larvae of 32 mm and 26 mm in *M. boulengeri* (26 mm SVL, MNHN 1991.3156 and 25 mm SVL, MNHN 1972.1930).

DISCUSSION

In amphibians, DUELLMAN & TRUEB (1986: 239-240) distinguish between sit and wait - foragers which ingest large prey and use little energy in obtaining food, and active foragers, which actively search for prey and consume small prey items. According to TOFT (1980a), (a) ant specialist frogs generally employ such an active foraging strategy, and (b) frogs cluster in two guilds based on this prey type distinction, ant specialists versus non-ant specialists. However, ant specialists may both be found among active foragers and sit-and-wait specialists, as pointed out by DONNELLY (1991), but comparative ethological studies on this subject are largely lacking.

Representatives of the aposematic genera of the Neotropical Dendrobatidae are ant specialists (e.g. TOFT 1995, CALDWELL 1996), and they are known to be active foragers (TAIGEN & POUGH 1983). In Madagascar, the genus *Mantella* has been

demonstrated to feed mainly on ants (74% of consumed prey items according to VENCES & KNIEL 1998), and they are known to be active, diurnal foragers (VENCES & al. 1998). They display a preference for small prey, which is eaten in large amounts (mean number of prey items per specimen = 52; maximum number of prey items found in one stomach = 131; VENCES & KNIEL 1998).

As indicated by the data presented in the present paper, the feeding preferences of *Mantella* are not shared by the species of *Tomopterna*, *Aglyptodactylus*, and *Boophis*, as well as most representatives of *Mantidactylus*. In all species studied, percentage of ant prey is lower than 50% (except *M. liber*), mean number of prey items per specimen is much lower (< 6) and the preference for small prey is less distinct than in *Mantella,* in which 76% of the prey items consumed were 3 mm in length or smaller (VENCES & KNIEL 1998). For comparison, in the *M. albofrenatus* complex which is similar to some *Mantella* in body size and general appearance, only 18% of the identified prey items belonged to these small size categories. None out of 774 prey items found in stomachs of *Mantella* specimens was longer than 5 mm (VENCES & KNIEL 1998). On the contrary, items of more than 10 mm length were identified in almost all species included in the present study. Some specimens ate very large prey, including vertebrates. This corresponds well with observations on a *Boophis goudoti* TSCHUDI, 1838 specimen which had consumed three frogs (GLAW & VENCES 1997), and with cursorial data (GLAW & VENCES 1994; VENCES & al. 1998) on *M. albofrenatus, M. mocquardi* ANGEL, 1929, *M. grandidieri* MOCQUARD, 1895, and *M. ulcerosus* which also consumed large prey (an earthworm of about 50 cm length in one *M. grandidieri,* a frog species that can attain 108 mm SVL). Although no standardized data on availability of different prey types in the frog's habitats are at hand, it is probable that most representatives of these genera are generalized feeders which do not actively discriminate against certain prey types.

An exception may be represented by *M. liber.* In this species, the proportion of ant prey was much larger (68%) and predominance of small prey (2-3 mm) was more expressed than in other *Mantidactylus*, also in comparison with species of similar body size (e.g. *M. boulengeri*: predominance of prey size class 6-10 mm). *Mantidactylus liber* belongs to the subgenus *Guibemantis* (see GLAW & VENCES 1994), one out of 12 subgenera within *Mantidactylus*. The phylogenetic relationships within the subfamily Mantellinae, which is composed by the two genera *Mantidactylus* and *Mantella*, are not yet solved. However, currently no characters are known which would support the monophyly of the large and heterogeneous "genus" *Mantidactylus*. By some morphological features (superficial femoral gland morphology, tadpole morphology - BLOMMERS-SCHLÖSSER & BLANC 1991), it can be hypothesized that some species of the subgenera *Guibemantis* and *Blommersia* are closely related to the genus *Mantella*. The fact that *M.* (*Guibemantis*) *liber* displays feeding habits more similar to those of *Mantella* than to those of other *Mantidactylus* would well fit into this hypothesis. However, it must be stressed that our data on *M. liber* are based on few identified prey items (19) only. Future studies should compare the foraging habits of this species to those of *Mantella* and should also include other species of *Guibemantis* and *Blommersia*.

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