Specialist or generalist? Feeding ecology of the Malagasy poison frog *Mantella aurantiaca*

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We studied the diet of a population of free-ranging *Mantella aurantiaca*, an alkaloid-containing poison frog from Madagascar. As in other poison frogs, this species is thought to sequester alkaloids from arthropod prey. Among prey, mites and ants are known to regularly contain alkaloids and mites appear to be a major source of dietary alkaloids in poison frogs. We predicted that mites and ants would constitute the most important prey item for these frogs. Prey inventories were obtained during the rainy season by stomach flushing 23 adult male and 42 adult female frogs from one population. Males had smaller body sizes than females and ate smaller prey items, but males and females displayed no differences in the number of prey items consumed. The numerical proportion of ants in most specimens was surprisingly low (11% in males and 15% in females), while mites were slightly more frequent (34% in males and 18% in females). Other prey items consumed in large proportions were flies and collembolans. Comparing the total of 5492 arthropod prey items with 1867 arthropods sampled from the frogs' leaf litter habitat, the proportion of prey classes did not significantly differ among the samples, indicating a low degree of prey electivity in this population. Our data suggest that not all poison frogs exhibit a continuous and active preference for feeding on ants and mites, but instead some may consume high proportions of ants due to a high abundance of ants in their environment.

Key words: Amphibia, ant feeding, Mantellidae, Madagascar, prey choice

INTRODUCTION

Specialization in foraging and feeding is known to be a major trigger for evolutionary novelty and adaptive radiation (Streelman & Danley, 2003). However, in amphibians, habitat rather than food choice tends to cause resource partitioning (Toft, 1985). In addition, the strongest factor influencing the radiations of anuran amphibians may be the striking diversification of reproductive modes and larval development (e.g. Wake, 1982; Duellman & Trueb, 1986; Dubois, 2005). Nevertheless, numerous frogs have evolved adaptations related to feeding mode (Nishikawa, 1999, 2000; Meyers et al., 2004). Among the most fascinating of these are the alkaloid-containing microphagous and myrmecophagous taxa. Alkaloids, which supposedly play a role in defence from predators, are found in the skins of poison frogs from four different families: the neotropical Dendrobatidae (various genera) and Bufonidae (*Melanophryniscus*), the Australian Myobatrachidae (*Pseudophryne*) and the Madagascan Mantellidae (*Mantella*) (Daly et al., 1987).

Among these alkaloid-containing taxa, the dendrobatids and *Mantella* especially are relatively small, diurnal and brightly coloured frogs. Their prey mainly consists of small arthropods, with ants and mites forming the majority of the diet (Simon & Toft, 1991; Toft, 1995; Caldwell, 1996; Vences & Kniel, 1998; Summers & Clough, 2001; Clark et al., 2005; Darst et al., 2005). Consequently, these frogs possess skull and tongue modifications such as the reduction of maxillary and vomerine teeth and tongue width that may be adaptations for ingesting small prey (Vences et al., 1998).

Recent research suggests these frogs take up their alkaloids from arthropod prey (e.g. Daly et al., 1994; Daly, 1998; Daly et al., 2002), with mites and ants contributing most of their alkaloids (Saporito et al., 2004; Clark et al., 2005; Takada et al., 2005; Saporito et al., 2007). Microphagous/myrmecophagous feeding and related specializations of skull and tongue, skin alkaloids, aposematic coloration and diurnal behaviour may constitute a closely linked suite of adaptations (Caldwell, 1996; Vences et al., 1998) for which the successive chain of evolutionary novelty remains largely undetermined.

The genus *Mantella*, comprising the Malagasy poison frogs, belongs to a radiation endemic to Madagascar and the Comoro island of Mayotte (Glaw & Vences, 2003; Vences et al., 2003). All are considered members of the family Mantellidae (Frost et al., 2006). *Mantella* contains about 17 species of brightly-coloured diurnal frogs inhabiting most of the bioclimatic and vegetation zones of Madagascar (Daly et al., 1996; Vences et al., 1999a). The colour patterns of several species, such as the black-yellow-orange *Mantella baroni* and *M. madagascariensis*, the black-orange *M. cowani*, and the uniformly orange *M. milotympanum* and *M. aurantiaca*, are probably aposematic. This attractiveness has made *Mantella*

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popular in the pet trade (Rabemananjara et al., in press) and has led to their use as flagship species for habitat protection (e.g. Zimmermann, 1996). Indeed, according to IUCN Red List categories, three species of *Mantella* are currently considered Vulnerable, two species Endangered and five species (*M. aurantiaca*, *M. cowani*, *M. expectata*, *M. milotympanum*, *M. viridis*) Critically Endangered (Andreone et al., 2005). Habitat destruction is believed to constitute the primary threat to these species, with the exception of *M. cowani*, which has also been overcollected for the pet trade (Andreone & Randrianirina, 2003; Vences et al., 2004).

Recent molecular data on *Mantella* has improved our understanding of their phylogeny and aided in the evaluation of their genetics for conservation purposes (Schaefer et al., 2002; Vences et al., 2004; Chiari et al., 2004, 2005; Vieites et al., 2006). Ecological studies on *Mantella* are needed for conservation purposes (Andreone et al., 2005), to advance our understanding of the convergent evolution of coloration (Chiari et al., 2004) and to identify how these frogs take up alkaloids from arthropods (Clark et al., 2005). Yet such field studies remain remarkably scarce. Besides anecdotal information on habitat and collection localities (e.g. Daly et al., 1996), only a few studies on distribution range, population density, predators and the reproduction of single species have been published (e.g. Heying, 2001a,b; Rabemananjara et al., 2005; Vieites et al., 2005). Preliminary data on diet of *Mantella* were collected by Vences & Kniel (1998) for *M. betsileo*, *M. haraldmeieri*, *M. laevigata* and *M. nigricans*. Recently, Clark et al. (2005) examined the stomach contents of *Mantella baroni*, *M. bernhardi* and *M. madagascariensis*, focusing on both the taxonomic composition and alkaloid content of prey. They found several alkaloid-containing ants and millipedes to be major components of *Mantella* food, indicating that prey specialization may have been responsible for the evolution of this frog's alkaloid uptake system.

In the present paper, we provide data on the prey composition of *Mantella aurantiaca*, an aposematic, uniformly orange species known to contain alkaloids (Daly et al., 1996). By comparing the stomach contents of these frogs with the food available in leaf litter samples, we hoped to determine whether the arthropods consumed by *Mantella aurantiaca* were due to active prey selection or to a background abundance of arthropods in the environment.

MATERIALS AND METHODS

Study site

The study was conducted in a forest bordering the natural flood plain of the Torotorofotsy swamp (18º52'29"S, 48º22'21"E; 960 m a.s.l.) near Andasibe, Madagascar. Vegetation in the area consisted of a sparse forest (approximately 70–90% canopy cover), with many vines and occasional shrubs. We defined one transect 100 m long and 10 m wide in an area of high *Mantella* abundance. Some 50 m of this transect bordered a stream. Fieldwork was carried out from 20 to 22 February 2004, corresponding to the end of the period of peak activity and reproduction for these frogs.

Frog processing

A total of 65 adult frogs was collected between 0600 and 1700, and processed immediately after capture at a nearby campsite. Specimens were sexed based on the presence or absence of the whitish femoral glands present in males only. For each frog, we measured snout–vent length (SVL) to the nearest 0.05 mm with callipers, and mass (M) to the nearest 0.05 g with a Pesola scale.

Stomach flushing was performed by inserting a small, flexible, bevel-ended human plastic catheter (Cook's precutaneous entry TFE catheter, 22 gauge) while the frog was inverted (Legler & Sullivan, 1979, Opatrný, 1980). During the insertion, water was pushed gently through the catheter with a large syringe (20 cm^3) to prevent injury to the frog. Once the catheter was inserted completely, gentle water pressure was applied until the stomach contents were expelled into a receptacle. This was done until no more prey items were expelled and tested by touching the ventral section of the frogs externally. Stomach contents were preserved in 70% ethanol. After stomach flushing, frogs were marked by toe-clipping and released along their transect of origin.

Leaf litter collection

Forty leaf-litter samples were taken from the same transect immediately after the final frogs were processed to avoid altering food availability over time. All of the leaf litter within a 1 m × 1 m quadrat was removed from the forest floor and placed in cloth mesh bags. Samples were weighed and divided in fractions of 0.05 kg, and were processed within a week of collection. Each fraction was placed for several days in a Berlese funnel trap. All leaves were subsequently checked by hand to collect any remaining arthropods. All arthropod specimens were preserved in 95% ethanol.

Identification of arthropods

Stomach content samples were examined in a Petri dish with a Harris micrometer/graticule scale (1 cm long, subdivided into 0.1 mm) (Griffiths, 1986; Griffiths & Mylotte, 1987). The lengths and widths of all organic matter, including organisms, particles and vegetation fragments, were measured to the nearest 0.05 mm. Lengths were considered the longest anterior to posterior apices, excluding appendages such as antennae, mandibles and ovipositors. Widths were measured at the widest girth perpendicular to length. Erected wings were not counted as part of the width. All organisms were identified to the lowest taxonomic level possible. The size of fragmented specimens was estimated based on other specimens with intact bodies. Arthropods from leaf litter samples were processed in the same manner.

All invertebrate length and width measurements were sorted into identification and size categories. Rough morphospecies were used in Diptera and consecutively numbered. Volumes of arthropod specimens were calculated using formulae (see Appendix) that best approximated the volumes of individual invertebrate cat-

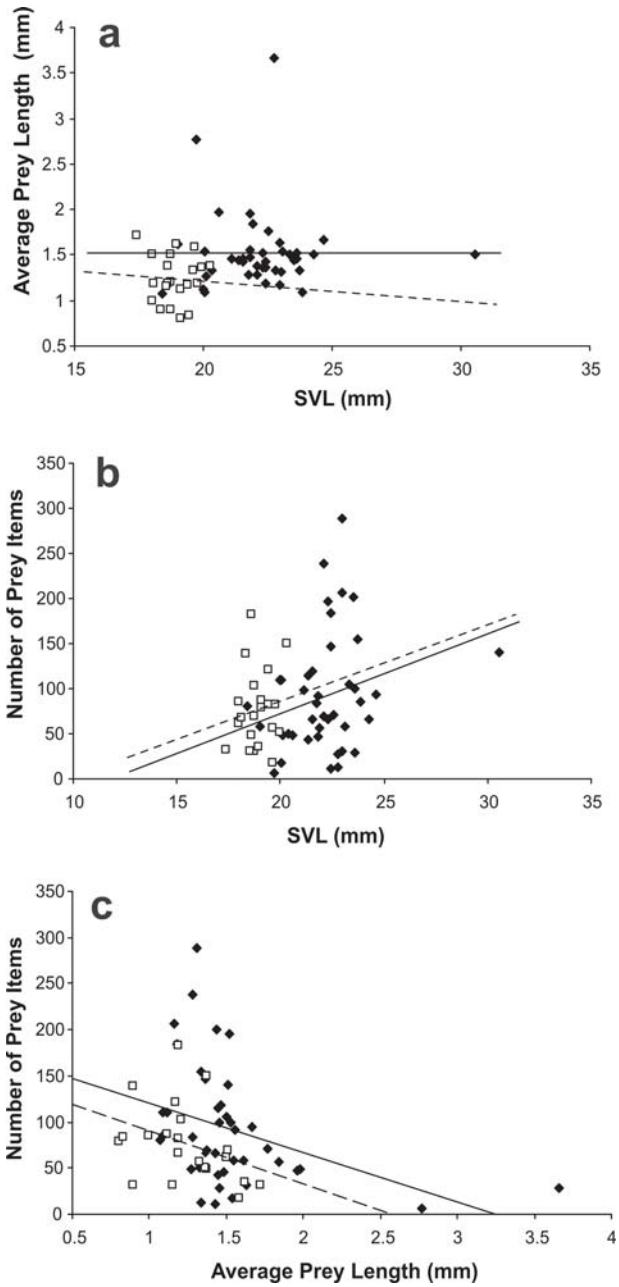

Fig. 1. The relationships between average prey length (APL), number of prey items (NPI) and snout–vent length (SVL) in male and female *Mantella aurantiaca*. Black symbols and continuous regression lines are females; white symbols and dashed lines are males. a) Relationship between APL and SVL. Slopes of regression lines: y=0.0006x+1.5131, P=0.988, for females; y=–0.0221x+1.6568, P=0.792, for males. The relationship is not significant if male and female data are analysed together (P=0.079). b) Relationship of NPI and SVL. Slopes of regression lines: y=8.7567x–101.81, P=0.092, for females; y=8.4975x–83.943, P=0.531, for males. The relationship is significant if male and female data are analysed together (P<0.05). c) Relationship of APL and NPI. Slopes of regression lines: y=–53.54x+174.05, P<0.05, for females; y=–57.318x+147.75, P=0.117, for males. The relationship is significant if male and female data are analysed together (P<0.05).

egories (Griffiths, 1986; Griffiths & Mylotte, 1987). Ants were identified to genus and morphospecies. The presence of each ant species per stomach content was assessed.

Statistical analysis

Data were entered into spreadsheets tracking frog number, date, time, field site location, SVL, M and number of prey items in the stomach (NPI). Individual frog prey dimensions were averaged to calculate average prey length (APL), average prey width (APW), average prey volume (APV) and total stomach content volume (SCV) for each individual frog. Separate calculations were made for unmarked and recaptured frogs. Values were compared between males and females, and between unmarked and recaptured frogs, using *t*-tests, to identify possible changes in food intake in frogs after stomach flushing. Consumed prey and dietary availability were compared using the Strauss Food Selection Index (Strauss, 1979) for prey occurrence, numerical abundance in percent and volume in percent (Hyslop, 1980). Correlation and linear regressions were performed with SPSS 10.0.

RESULTS

Prey use in relation to frog sex and size

We obtained stomach contents from 65 frogs, of which 23 were males and 42 were females. Thirteen of these frogs were recaptured and stomach-flushed a second time. The number of prey items and average stomach content volume were found to be significantly lower in recaptured frogs of both sexes (*t*-tests, P<0.005), although the frogs did not differ significantly in size measurements. Recaptured frogs also appeared to have consumed smaller prey, but the differences were not significant (P=0.056). Mean NPI±SD was 24.4±40.5 in recaptured frogs vs 84.5±59.6 in unmarked frogs. Mean SCV was 3.2±4.1 mm^3 vs 13.1±9.5 mm^3. This is probably due to the short time span between captures, which may not have been enough for the frogs to reach "average" levels of food items. Consequently, all further calculations were based on first-time capture data.

SVL was 17.4–20.3 mm (mean = 19.0, SD = 0.8 mm) in males, 18.4–30.6 mm (mean = 22.2, SD = 1.9 mm) in females. Sixty-three of the unmarked frogs contained prey in their stomachs; two males had empty stomachs. In total, 5492 prey items were identified, 3880 items in females, 1612 items in males. Male frogs were smaller than females (*t*-tests for SVL, MV, MH; P<0.001 for all comparisons) and ate smaller, less voluminous prey items than females (*t*-tests for APL, APV; P<0.05 for all comparisons). However, females and males displayed no differences in the number of prey items consumed (*t*-test for NPI; P=0.151). Comparing all prey items found in males with those in females, significant differences were found in prey length (*t*-test on IPL; P<0.001) and prey volume (*t*-test for IPV; P<0.05). Average length of all prey items consumed ±SD was 1.19±0.82 mm (0.2–8.6 mm) in males and 1.41±1.12 mm (0.2–47 mm) in females. Average volume ±SD was 0.12±0.64 mm^3 in males and 0.17±0.73 mm^3 in females. The smallest prey items in males and females were mites and collembolans. The largest observed prey items

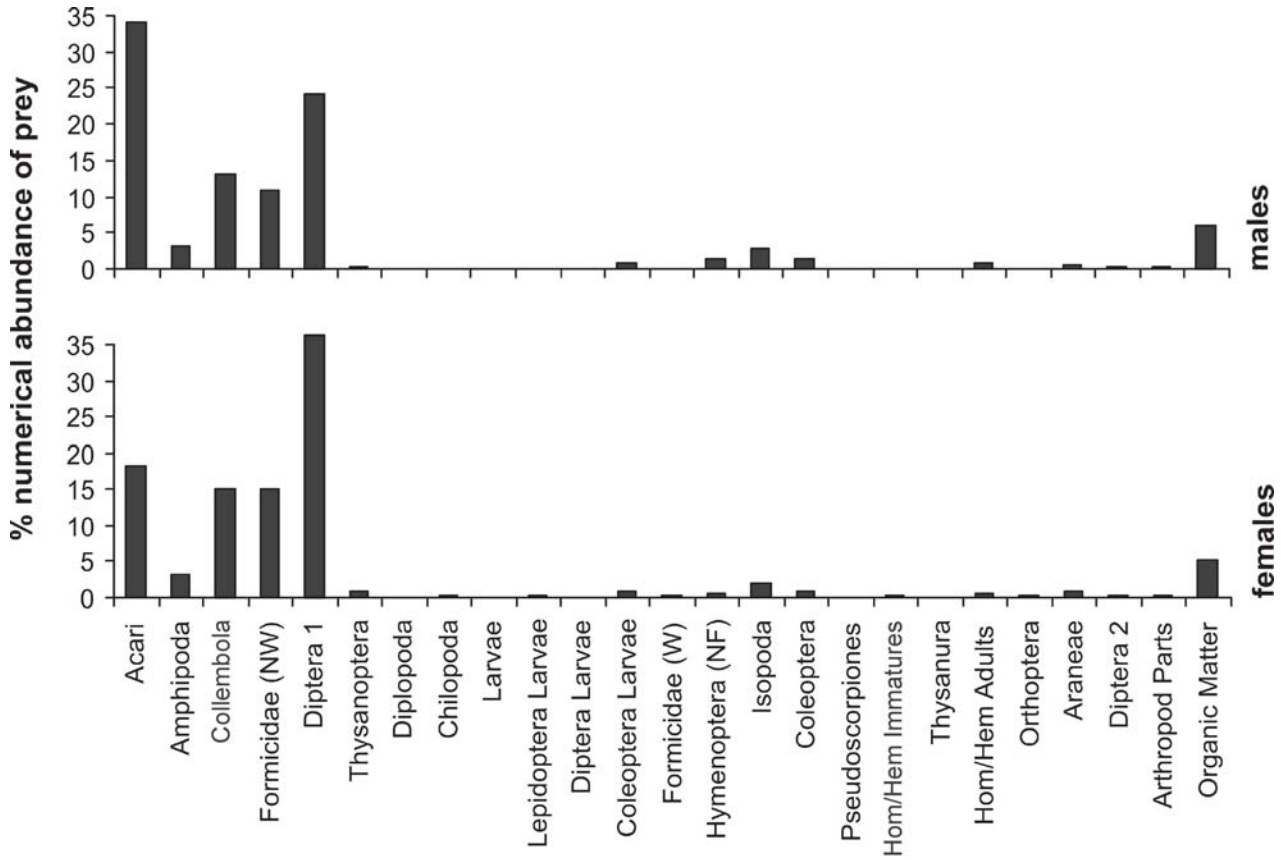

Fig. 2. Comparison of numerical abundance of different prey items in the diet of male and female *Mantella aurantiaca*. Values are averages of percentages for individual stomach contents, and are correlated between sexes (Spearman rank correlation: r_s=0.842; P<0.01). Abbreviations: Homoptera (Hom), Hemiptera (Hem), non-Formicidae (NF), winged (W), non-winged (NW).

were insect larvae, isopods, beetles, centipedes and amphipods of 6–9 mm, as well as one 47 mm centipede found in a female frog. Of all prey items, 95.8% had lengths of <3 mm, 82.9% were <2 mm and 36.5% <1 mm.

Our data show no obvious trends for larger frogs to eat larger prey (Fig. 1a). Although females consumed larger prey, this was apparently not due to their larger sizes. However, both sexes showed an increase in NPI consumed as SVL increased (Fig. 1b). APL and NPI were negatively correlated both when considering males and females together, and for female data alone (P<0.05), indicating that individuals that consumed larger prey had on average consumed fewer prey items (Fig. 1c).

All prey categories were found in the stomachs of both males and females, with the exception of winged Formicidae and Lepidoptera larvae, which were found exclusively in females. The percent occurrence of prey categories, as well as percentage and volume of prey items per category (Spearman rank correlation, P<0.01; Fig. 2), was highly correlated between males and females. Females ate a larger number of soft-bodied Diptera 1, while males consumed larger quantities of mites than females. Among males, mites were the most frequent prey items (34.1%), followed by flies (24.4%), collembolans (13.0%) and ants (11.3%). In females, flies were the most frequent prey item (36.1%), followed by mites (18.1%), ants (15.3%) and collembolans (14.7%). However, in both males and females, ants made up the highest proportion of stomach content volume (26.3% and 28.8%, respectively), followed by flies (22.4% and 24.6%, respectively).

Prey use in relation to prey availability

Arthropod availability and prey selection was based on data from 11 leaf-litter samples with 1867 individual potential prey items, and compared against the same 65 frog samples (42 females and 23 males) containing a total of 5492 prey items in their stomachs. All leaf-litter and stomach samples contained mites, collembolans and non-winged ants. Flies (Diptera 1) were rare in leaf-litter samples but common in stomach samples. This discrepancy may have been due to a methodological bias, as the flies may have evaded capture within the leaf-litter samples. Other flies (Diptera 2), winged ants and thysanurans were likewise absent from leaf-litter samples, suggesting either low numbers or evasion of capture. Stomachs lacked the prey classes Diptera 3, Blattodea, Dermaptera and Nematoda, although some large, unidentified arthropod parts present in some frog stomachs may have belonged to Blattodea. Leaf-litter and stomach content samples were correlated in terms of occurrence, numbers and volumes of prey categories (Spearman rank correlation, P<0.05). In all three categories, frog diet and prey availability in leaf litter mirrored each other (Figs 3–4; Table 1). The Strauss Food Selection Index (Strauss, 1979) indicated low electivity regarding all prey classes for both numbers (Fig. 5) and volumes of arthropods. There may

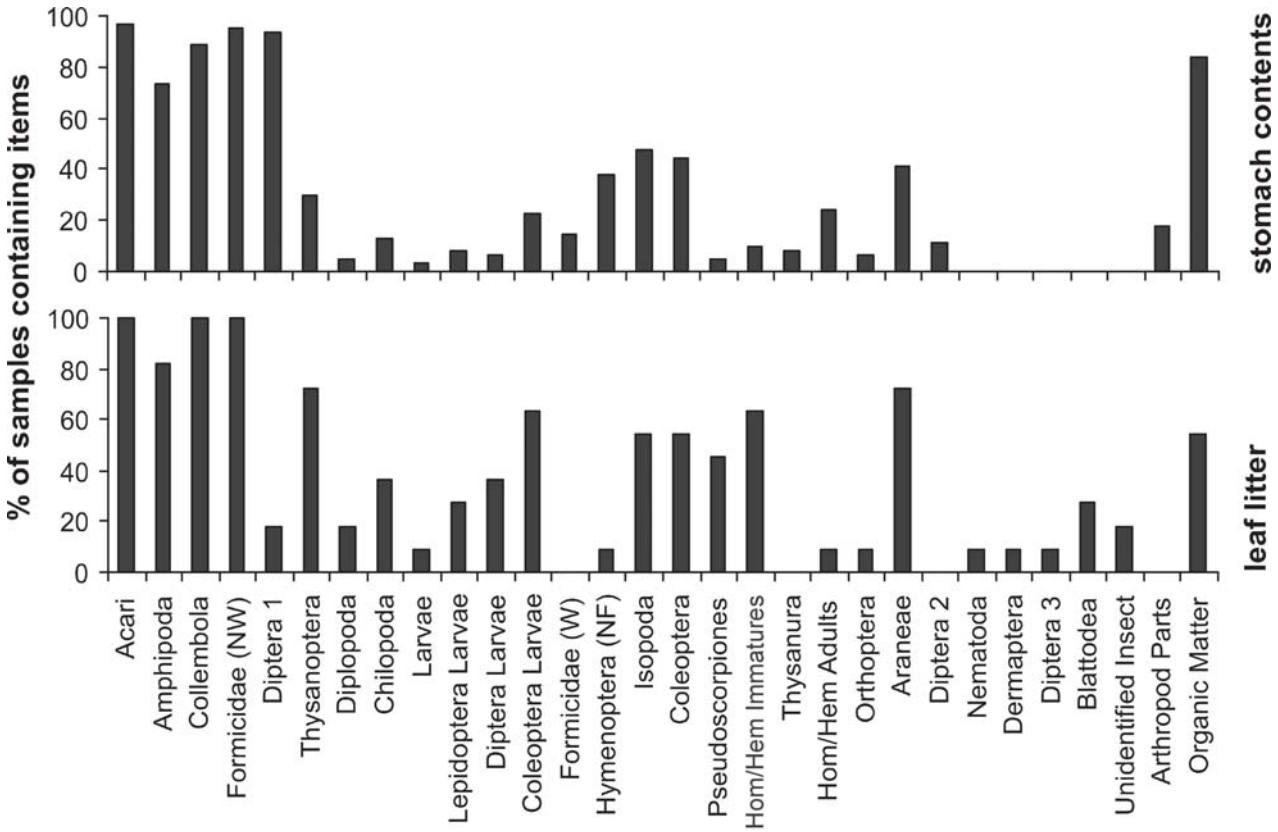

Fig. 3. Comparison of prey consumed with prey availability. Columns show the percentage of stomach and litter samples that contained different prey items. Data are correlated (Spearman rank correlation: r_s=0.564; P<0.01). Abbreviations as in Fig. 2.

also have been a negative election of mites and a positive election of flies (Diptera 1), but the latter may be due to methodological issues (see above).

Stomachs contained ants from nine genera: *Crematogaster* (1 morphospecies), *Cataulacus* (1), *Anochetus* (1), *Paratrechina* (1), *Hypoponera* (2), *Strumigenys* (3), *Tetramorium* (6), *Monomorium* (4) and *Pheidole* (7). Frequency of occurrence was highest in one morphospecies of *Pheidole* (present in 48 stomach contents) and two morphospecies of *Monomorium* (present in 45 and 24 stomach contents). All other ant morphospecies were present in ten or fewer stomach contents only.

DISCUSSION

Prey electivity in *Mantella aurantiaca*

Our data indicate that the prey of *Mantella aurantiaca* consists mainly of arthropods of small size, different from most other mantellid species where numerous large prey items are found (Vences et al., 1999b). Although ants were not the most numerically common prey items (14%), they comprised the bulk of the prey consumed (28%) in terms of volume. Mites, which have recently been shown to be a major source of dietary alkaloids in poison frogs (Takada et al., 2005; Saporito et al., 2007), were present in high numbers (23%) but only made up 5% of the volume of the stomach contents. However, it is insufficiently understood whether volume or individual numbers of a particular prey is more important to determine alkaloid content and composition of poison frogs. If all individuals of one prey type contain similar alkaloids in similar concentration, and alkaloids are stored in the skins of the frogs for long periods, then volume is probably most important. If only some individuals of a certain prey category contain alkaloids, prey individuals differ in the concentration of contained alkaloids, and/or alkaloids are stored only for a limited time in the skins of the frogs, then it is probably more important that the frogs eat large numbers of this prey category, in order to ensure that at regular intervals some prey individuals with high alkaloid concentration are consumed.

Ant species of *Tetramorium* were present in twelve stomach contents (summarized for the four morphospecies of this genus). One species of this genus had previously been found to contain two different pumiliotoxin alkaloids (Clark et al., 2005). A species of *Paratrechina* was present in a single stomach; these ants are known to contain a variety of alkaloids, and together with other species of formicine ants could potentially contribute to the dietary alkaloids of *Mantella aurantiaca*. Several other arthropods found in the stomach contents, such as millipedes and beetles, could potentially provide dietary alkaloids as well (e.g. Ayer and Browne, 1977; Daly et al., 2002; Saporito et al., 2003; Clark et al., 2005).

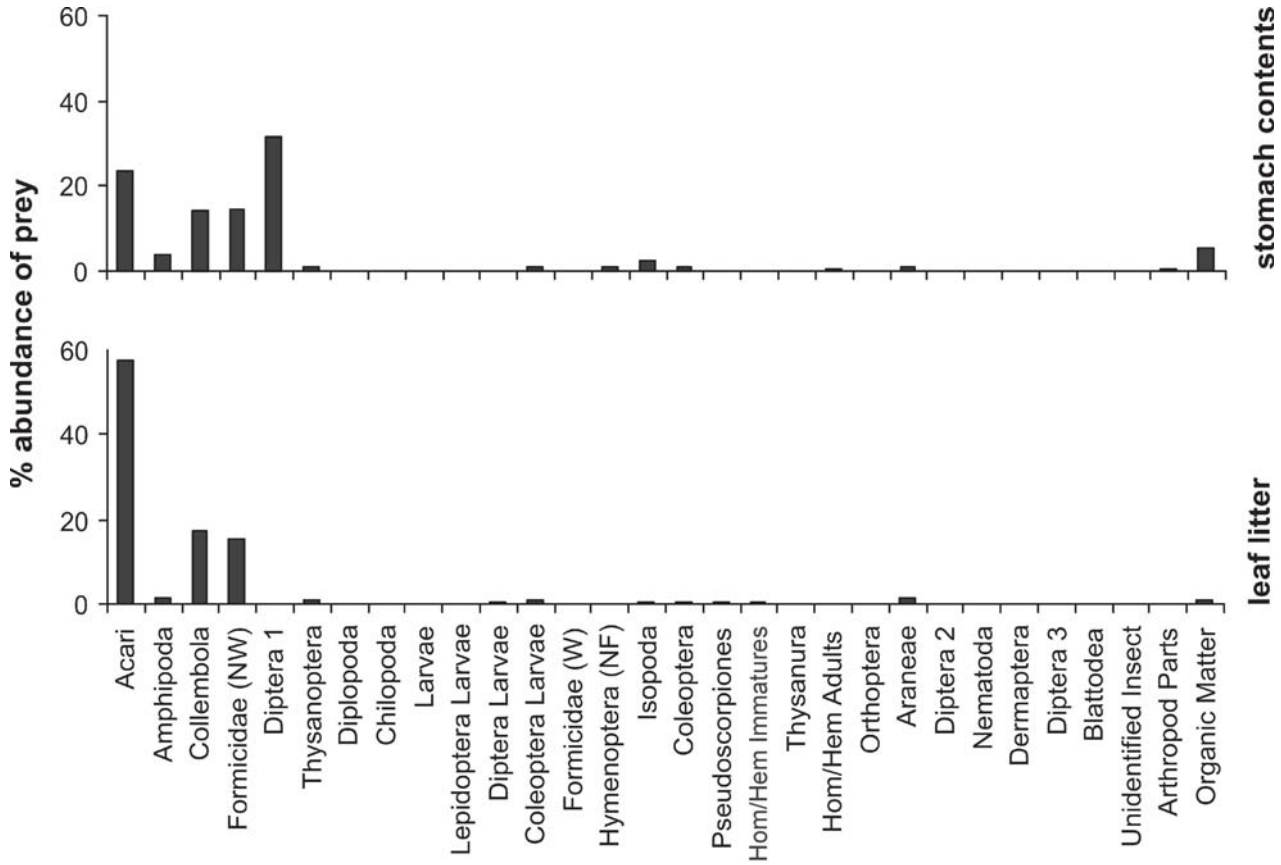

Fig. 4. Comparison of prey consumed with prey availability. Columns show the percentage numerical abundance of prey items in stomachs and leaf litter. Data are correlated (Spearman rank correlation: r_s=0.613; P<0.01). Abbreviations as in Fig. 2.

Prey size did not appear to be a function of frog body size. Though larger frogs eat more prey, it is of the same average size as prey eaten by smaller frogs. This contrasts with data from other studies which found frogs of greater snout–vent length consuming fewer but larger prey (e.g. Berry, 1966; Brooks, 1982; Hirai, 2002; Hodgkinson & Hero, 2003; Ramírez-Bautista & Lemos-Espinal, 2004). The fact that large and small individuals of *Mantella aurantiaca* consumed arthropods of the same average size indicates little preference for different-sized prey.

This is confirmed by the comparisons of prey in the leaf litter versus the stomach contents. The electivity analysis provided little evidence for prey selection. Indeed, cases where preference was apparent (e.g. for flies), may in fact be artefacts of our collection method. Thus *Mantella aurantiaca* appeared to consume prey in proportion to its availability. The one distinct exception were mites – these were consumed at lower proportions, either because 1) they are difficult to find due to their small size and cryptic habits, or 2) there is active discrimination against such small prey. Few large prey items were consumed, but such large arthropods were apparently also rare in the leaf litter. Hence, *M. aurantiaca* followed a microphagous – but not a myrmecophagous – foraging mode, but this pattern is a reflection of the abundance of small prey in the environment at the study site and in the study period. MacNally (1983) studied a similar case, in which two species of *Ranidella* mainly consumed small prey below 1.5 mm in length, but with a very low proportion of ants, reflecting the patterns of availability of different prey types and prey sizes.

Prey electivity of other *Mantella*

Previously published results have observed a high percentage (74%) of ants in stomachs of *Mantella haraldmeieri, M. nigricans, M. laevigata* and *M. betsileo* (Vences & Kniel, 1998), and 67% ants in *M. baroni, M. bernhardi* and *M. madagascariensis* (Clark et al., 2005). The percentages of ants consumed by *M. aurantiaca* are much greater than the proportion of ants consumed by most other mantellid frogs analysed (genera *Aglyptodactylus, Boophis, Gephyromantis, Laliostoma* and *Mantidactylus*), usually because many of these species consume much larger prey (Vences et al., 1999b). At first glance a comparison of our results with these published data seems to indicate an important difference between *M. aurantiaca* and other *Mantella* species: whereas congeneric species appear to be ant specialists, *M. aurantiaca* does not display such a preference.

However, previous studies did not include data on food availability, and therefore it is not yet possible to determine whether the dietary pattern of *Mantella aurantiaca* is common among other species in this genus. Our data do not support the idea of *Mantella aurantiaca* as a specialist, although this species may display different feeding patterns with clear preference for ants in other populations or in other seasons. However, it

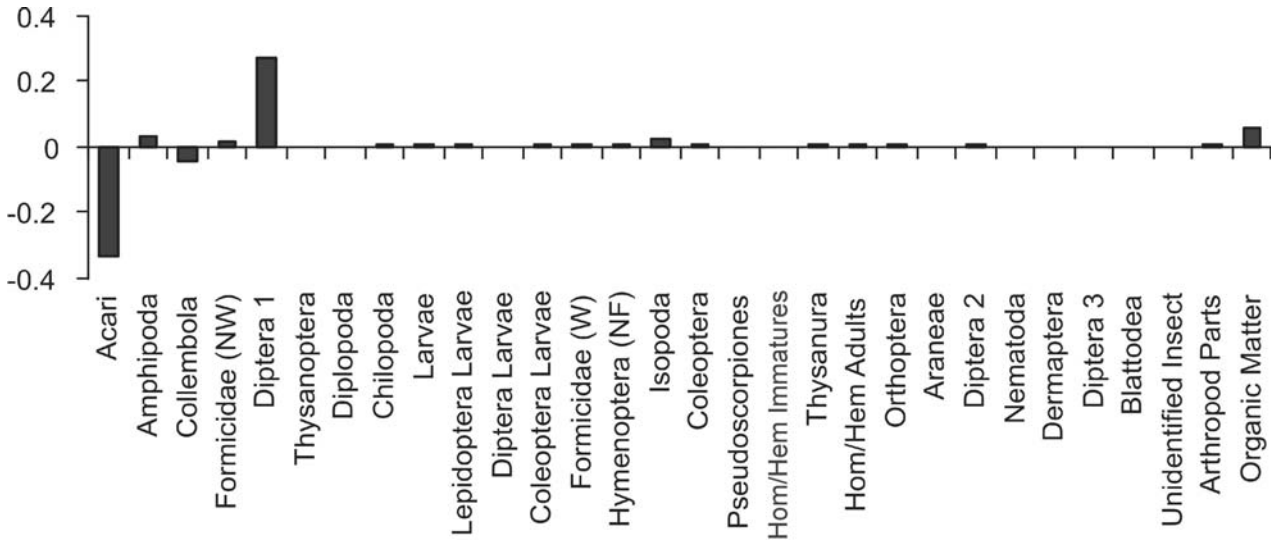

Fig. 5. Strauss Food Selection Index for numerical abundance of prey found in leaf litter and frog stomach samples. Abbreviations as in Fig. 2.

is also possible that the high proportion of ants found in some *Mantella* species simply reflects a high abundance of ants in their environment. Indeed, a study currently underway by T. Razafindrabe and co-workers indicates that in many *Mantella* populations, regardless of breeding season, the numerical proportion of ants consumed was lower than that previously encountered (about 70%; Vences & Kniel, 1998; Clark et al., 2005), although these results are based on far fewer individuals per population than our study. In the study by Vences & Kniel (1998), no marked preference for small-sized prey (fruit flies) versus larger prey (crickets) was found in various species of *Mantella*, while such a preference was more obvious for three species of dendrobatid frogs of the genera *Dendrobates* and *Phyllobates* (especially for *D. leucomelas*). Although these experimental results on captive animals may be biased by the habituation of these specimens to particular kinds of prey, the results would be in agreement with less feeding specialization in *Mantella* as compared to dendrobatids.

Temporal variation in prey

Most *Mantella* habitats in Madagascar are characterized by marked seasonality, and the frogs undergo at least partial hibernation (during the cool, dry austral winter). This may involve a trade-off between the need to accumulate fat reserves rapidly and the selective uptake of alkaloid-containing prey for chemical defence. This hypothesis would predict different strengths of prey electivity during different periods of frog activity. Frogs may change their diet, and possibly also their diet preferences, in different time periods, if, for example, preferred prey become seasonally less abundant. This scenario has already been suggested for other tropical communities studied during whole-year periods (Whitfield & Donnelly, 2006). During our study, the population of *M. aurantiaca* was still reproducing but was getting close to the end of the reproductive season, and this may be one explanation for the low prey electivity encountered, as adults may spend less time searching for prey and rely more on the food they can encounter close to their breeding grounds. Long-term variations in the alkaloid profiles of populations of dendrobatids have already been observed by Daly et al. (1987), and recent studies by Saporito et al. (2006) demonstrate large seasonal fluctuations in alkaloid profiles of populations of *Oophaga* (previously *Dendrobates*) *pumilio* from Panama that may reflect different food composition or different feeding strategies at different times of the year. Long-term temporal variation in alkaloid profiles has also been observed in *Mantella baroni* (Clark et al., 2006), and is hypothesized to reflect turnover in arthropod communities.

Ant specialists versus ant avoiders

Based on observations mainly of lizard data, Huey & Pianka (1981) remarked that species are either widely foraging or sit-and-wait predators (but see Perry & Pianka, 1997; Perry, 1999). Moreover, these behaviours correlate with different types of prey consumed; widely foraging species concentrate on prey that is sedentary, unpredictably distributed and clumped, such as ants and termites. Similarly, based on large surveys of consumed and available prey for diurnal tropical litter frogs, Toft (1980a,b, 1981) distinguished between active foragers, which elected ants, and sit-and-wait foragers, which avoided ants. A weak avoidance of ants was also reported by Hirai & Matsui (2000) for *Glandirana rugosa*, which had a high numerical abundance but a low volumetric proportion of ants in its diet, and consumed a lower proportion of ants than was found in the environment. Among nocturnal anurans, species of the family Microhylidae may be ant and mite specialists (Toft, 1981), which is consistent with other studies (e.g. Berry, 1965) and with their specialized tongue morphology and feeding behaviour (Meyers et al., 2004).

In dendrobatids, Toft (1980a) found that the position of these frogs along a specialist–generalist continuum was similar irrespective of the type of calculation applied: electivity, or simple niche breadth calculated from proportions of prey categories. Consequently, Darst et al. (2005)

Table 1. Total numbers and percentages, and volume (in mm^3) and percentage of volumes, of the most common prey categories found in the stomach contents of male and female *Mantella aurantiaca*, and in leaf litter samples from frog habitat. Organic matter refers to undetermined remains, probably of accidentally consumed leaf litter.

	Prey numbers (males)	Prey numbers (females)	Prey in leaf litter numbers	% prey numbers (males and females)	% leaf litter numbers	Prey volumes (males)	Prey volumes (females)	Leaf litter volumes	% prey volumes (total)	% leaf litter volume
HEXAPODA										
Thysanura	1	4	0	0.1	0.0	0.0	0.3	0.0	0.0	0.0
Collembola	209	572	309	14.2	16.6	15.4	51.8	3.6	7.9	1.2
Thysanoptera	6	24	20	0.5	1.1	0.2	1.0	0.8	0.1	0.3
Homoptera/Hemiptera: adults	10	22	1	0.6	0.1	3.5	8.4	0.1	1.4	0.0
Homoptera/Hemiptera: immatures	1	7	8	0.1	0.4	0.1	3.8	1.6	0.5	0.6
Orthoptera	1	3	1	0.1	0.1	0.2	2.3	0.4	0.3	0.1
Hymenoptera: Formicidae	182	593	348	14.1	18.7	52.6	187.5	90.4	28.2	31.3
Hymenoptera: Formicidae winged	0	13	0	0.2	0.0	0.0	3.5	0.0	0.4	0.0
Hymenoptera: others	19	23	1	0.8	0.1	5.7	4.1	0.5	1.2	0.2
Diptera 1	393	1402	2	32.7	0.1	44.7	160.7	0.1	24.1	0.0
Diptera 2	4	7	0	0.2	0.0	0.6	2.1	0.0	0.3	0.0
Coleoptera	14	26	12	0.7	0.6	1.2	4.7	19.4	0.7	6.7
Larvae: Lepidoptera	0	6	3	0.1	0.2	0.0	19.4	15.1	2.3	5.2
Larvae: Diptera	2	3	4	0.1	0.2	0.2	0.3	6.2	0.1	2.1
Larvae: Coleoptera	9	21	14	0.5	0.8	26.7	23.4	60.8	5.9	21.1
Larvae: undetermined	1	1	1	0.0	0.1	0.2	12.4	0.0	1.5	0.0
Other Hexapoda	0	0	5	0.0	0.3	0.0	0.0	7.1	0.0	2.5
CRUSTACEA										
Amphipoda	51	124	25	3.2	1.3	16.0	46.0	29.9	7.3	10.4
Isopoda	52	69	8	2.2	0.4	5.7	18.3	6.8	2.8	2.4
Myriapoda										
Diplopoda	1	2	2	0.1	0.1	0.3	0.7	0.6	0.1	0.2
Chilopoda	2	10	4	0.2	0.2	0.6	37.5	4.7	4.5	1.6
Arachnida										
Acari	550	703	1051	22.8	56.4	15.3	30.8	22.3	5.4	7.7
Araneae	9	31	21	0.7	1.1	1.2	4.0	16.1	0.6	5.6
Pseudoscorpiones	1	2	12	0.1	0.6	0.0	0.1	0.2	0.0	0.1
OTHERS										
Arthropoda parts: undetermined	4	16	0	0.4	0.0	2.7	11.3	0.4	1.6	0.1
Organic matter	90	196	12	5.2	0.6	6.9	16.4	1.5	2.7	0.5
Total	1612	3880	1864	100	100	200.0	650.8	288.6	100	100

used values of niche breadth as proxies for dietary specialization in dendrobatid poison frogs. In dendrobatids, myrmecophagy appears to have evolved multiple times, and in most cases was associated with the recurrent evolution of noxiousness and aposematism (Caldwell, 1996; Summers & Clough, 2001; Darst et al., 2005). However, Darst et al. (2005) also discussed the case of *Allobates zaparo*, in which stomach content analyses from different populations gave conflicting results regarding the proportion of ants consumed (74% vs 11%, 26% and 34%). This species is a phylogenetically basal species of dendrobatid (e.g. Vences et al., 2003; Santos et al., 2003), and its variability in feeding strategies may therefore be greater than in the more specialized dendrobatids (e.g. the genus *Dendrobates sensu lato*).

Our results suggest caution if a generalist–specialist continuum of myrmecophagy or microphagy is to be based on niche breadth data alone: niche breadth may in some poison frog species or populations reflect a true dietary specialization in terms of positive electivity of certain prey categories, and in other cases may just reflect frequencies of prey in the environment. Comparing data

from dendrobatids to those of other alkaloid-containing frogs may also reveal that the generalist versus specialist continuum and the active-search-foraging versus sit-and-wait foraging continuum are not always in full correspondence with each other. *Mantella* are clearly actively foraging and diurnal species, and like dendrobatids show continuous small movements. Food capture is mostly by tongue only (versus fully leaping forward), a technique probably associated with lower metabolic costs (Toft, 1981). Nevertheless, *Mantella*, at least on some occasions, do not seem to actively elect small prey or ants, and how strongly this trend varies among species, populations and seasons remains to be studied.

ACKNOWLEDGEMENTS

We are grateful to Olivier Sam Mamy and Jean-Noel Ndriamiary of the Mitsinjo team in Andasibe for their help in the field. We further thank Edouard Randriamitso and Nandi Fatroandriantjafinontjasolokitova for field companionship, Rainer Dolch for logistical assistance, DICE for funding, David Sewell for support, and Laura, Mary and David Eklund, and David and Marvalee Wake for logistical support in California. Ralph A. Saporito and several anonymous reviewers helped to significantly improve previous manuscript drafts. The Malagasy authorities provided authorizations for research and specimen exports under a cooperation accord between the universities of Amsterdam and Antananarivo, and the Association National pour la Gestion des Aires Protegées–ANGAP. Financial assistance to M. Vences was provided by the Volkswagen and BIOPAT foundations. D.R. Vieites was supported by a University of Vigo grant for research in foreign countries. B.L. Fisher was supported in part from NSF DEB-0344731.

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Accepted: 3 October 2007

APPENDIX

Formulae used to calculate volumes of prey items. Abbreviations as follows: height (H), width (W), length (L).

Formula	Prey categories
$V=\pi r^2H$	Collembola Coleoptera larvae Diplopoda Diptera 1, 2, and 3 Diptera larvae Formicidae (winged) Hymenoptera (non-winged) Insect larvae Lepidoptera larvae
$V=0.1LW$	Organic matter (vegetation)
$V=(2/3)\pi r^2H$	Formicidae (non-winged)
$V=(1/3)\ \pi r^2H$	Acari
$V=\pi r^2H(1/2)$	Chilopoda Thysanoptera
$V=(1/2)(1/3)\ \pi r^2H$	Thysanura
$V=\pi(4/3)\times(0.5L)\times(0.5H)\times(0.25H)\times(1.5)$	Amphipoda Blattodea Coleoptera Dermaptera Isopoda Pseudoscorpiones Unidentified insects
$V=\pi(4/3)\times(0.5L)\times(0.5W)\times(0.25W)$	Homoptera/Hemiptera, adults and immatures
$V=\pi(4/3)(0.5L)^2\times(0.5W)$	Organic matter (seed-like 2)
$V=\pi(4/3)(0.5L)\times(0.5W)^2$	Araneae Arthropod parts Organic matter (dirt) Organic matter (seed-like 1) Orthoptera