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Author(s): Joelisoa Ratsirarson and John A. Silander, Jr.
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Structure and Dynamics in *Nepenthes madagascariensis* Pitcher Plant Micro-Communities[1]

Joelisoa Ratsirarson[2] and **John A. Silander, Jr.**

Department of Ecology and Evolutionary Biology, The University of Connecticut, Storrs, Connecticut 06269-3042, U.S.A.

ABSTRACT

The pitchers of *Nepenthes madagascariensis* are visited by a wide variety of insects attracted to the bright color of the pitcher, the nectar secreted around its opening and the odor of the fluid. The insect visitors appear to become disoriented over time and with increasing likelihood fall into the pitcher and drown.

The pitchers form a temporary habitat functional for about three months. Several specialized arthropods including mosquito larvae (*Uranotaenia bosseri, U. belkini*), mites (*Creutzeria* sp.), and frit fly larvae (*Chloropidae*) complete their life cycle in the pitcher and depend directly or indirectly on the drowned insects falling into the pitcher. Colonization by these arthropods varies spatially and temporally between the two forms of pitchers (juvenile, rosette form and adult form). Mites (*Creutzeria* sp.) show a phoretic relationship in colonizing new pitchers by clinging to adult frit flies that emerge from the pitcher's fluid. Food web interactions in the *Nepenthes madagascariensis* pitcher are more complex than those reported by Beaver (1985).

RESUMÉ

Les urnes de *Nepenthes madagascariensis* sont visitées par de différents types d'insectes attirés par la couleur de l'urne, par le nectar sécrété autour de son ouverture et par l'odeur du liquide. Les insectes visiteurs semblent être de plus en plus désorientés, et leur chance de tomber dans l'urne augmente en fonction du temps.

Les urnes forment un habitat temporaire et fonctionnel pour trois mois. Plusieurs arthropodes spécialisés, y compris des larves de moustiques (*Uranotaenia bosseri, U. belkini*), des mites (*Creutzeria* sp.), des larves de moucherons (Chloropidae) vivent à l'intérieur de l'urne et dépendent directement ou indirectement des insectes tombant dans l'urne. La colonisation de ces arthropodes varie dans le temps et l'espace entre les deux types d'urnes (forme juvenile et forme adulte). Les mites (*Creutzeria* sp.) montrent une association phorétique pour coloniser l'urne en s'accrochant sur les mouches adultes (Chloropidae) qui émergent du liquide. Les interactions entre les organismes associés au *Nepenthes madagascariensis* semblent plus complexes que celles publiées par Beaver (1985).

Key words: colonization; community; ecology; food web; insects; Madagascar; Nepenthes; *pitcher plant.*

INTRODUCTION

MADAGASCAR WAS THE SITE where *Nepenthes* was first discovered by Flacourt in the middle of the 17th century (Wunschmann 1872). However, virtually nothing is known of either the ecology of these plants in Madagascar, or the community structure and dynamics of the organisms associated with the pitchers. Two endemic species of *Nepenthes* occur in Madagascar: *Nepenthes masoalensis* and *N. madagascariensis*. These comprise the westernmost extension of *Nepenthes*' distribution (Beaver 1983, 1985).

Nepenthes madagascariensis is restricted to the coastal, eastern region from Tamatave to Fort Dauphin (Decary 1928, Humbert 1954, James, 1988). The species can be locally abundant but usually occurs in widely scattered populations.

The purpose of the study was to determine the structure and dynamics of the community of organisms associated with *Nepenthes madagascariensis* pitchers. Specifically, the study examined the type, behavior and abundance of arthropods living inside the pitcher as related to the pitcher's attributes, the colonization of pitchers by these arthropods, and the feeding (food web) interactions among consumers and resources associated with pitcher micro-communities.

The type, behavior and abundance of the pitcher arthropods provide information necessary to understand the dynamics and food web interactions within pitcher micro-communities (Pimm 1982,

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[2] Current address: Yale School of Forestry and Environmental Studies, 205 Prospect St., New Haven, Connecticut 06520.

Lawton & Warren 1988). Because they are easily manipulated, *Nepenthes* pitchers provide an ideal, model microcosm for understanding community level processes (Beaver 1983, Frank & Lounibos 1983, Givnish *et al.* 1984, Naeem 1988).

STUDY SITES

The genus *Nepenthes* (Nepenthaceae) contains 65–70 described species, with a center of distribution in the Indo-Malay region (Beaver 1983). All species of *Nepenthes* form pitchers as modified leaf tips, borne on tendrils. Endemic species occur at the western and northern margins of the range of the genus in the Seychelles, Sri Lanka, India and Madagascar (Beaver 1985).

The liquid inside the pitcher is produced before the pitcher opens. Fluid production continues after the pitcher opens and is diluted by rainwater. *Nepenthes* spp. pitchers in general are supplied with glands, including nectaries which serve to attract prey and digestive glands which secrete the fluid and enzymes into the pitcher (Schmucker & Linneman 1959, Juniper *et al.* 1989). Nectaries are found on the inner edge of the peristome (pitcher opening) and under the surface of the lid of the pitcher. Digestive glands are located in the lower one-third to one-half of the walls of the pitcher. The secreted enzymes reported for the full range of *Nepenthes* species include proteases, lipases, esterases, ribonucleases, acid phosphatases, and possibly chitinase (Heslop-Harrison 1978, Slack 1979). Nectar and digestive glands have the same anatomical structure (Lloyd 1976, Juniper *et al.* 1989). The digestive glands also take part in the uptake of the products of digestion. Among several species of *Nepenthes* studied here and elsewhere, part of the incoming food to the pitcher is used by organisms living in the pitcher fluid and the part by the plant (Beaver 1983).

The strategy of *Nepenthes madagascariensis* pitchers in attracting prey resembles that of a flower attracting pollinators (see also Joel 1988). The pitchers commonly display bright red and yellow color patterns, secrete copious nectar around the peristome (Fig. 1A), and possess a distinctive odor (pers. obs.).

The main study site was located in Mandena, 12 km North of Taolanaro (Fort Dauphin) in the southeast of Madagascar. The population of *Nepenthes madagascariensis* at this site was locally abundant. The mean annual precipitation is 1800 mm, well distributed throughout the year. Mean annual temperature is 22°C (Madagascar National Weather Service, unpub. data). The habitat is a grassland or heath shrubland (Fig. 1B, C), degraded from an original moist lowland forest, found on nutrient-poor, acidic sandy soils, currently dominated by *Ravenala madagascariensis* (Strelitziaceae), *Pandanus* spp. (Pandanaceae) and *Phillippia* spp. (Ericaceae).

METHODS

The life span of a pitcher was determined by marking 60 unopened pitchers, and observing them over their lifetime. Morphologically, *Nepenthes madagascariensis* plants can be divided into two types: the juvenile rosette form with short goblet-shaped pitchers, and the adult form with long, narrow, trumpet-shaped pitchers (Fig. 1D).

To characterize the differences between the two types of pitchers, comparative attribute measurements were taken on 105 individual pitchers (52 goblet pitchers and 53 trumpet pitchers) at ages between 30–40 days for trumpet pitchers, and 7–14 days for goblet pitchers. Individual pitchers were chosen randomly along a 100 m transect. The measurements included total volumetric capacity of the pitcher, volume of the liquid inside, height of the pitcher above the ground, and numbers of individuals for each species of arthropod living inside the pitchers (mosquitoes, flies and mites). The capacity of the trumpet pitcher was measured assuming that the pitcher can be described as a cone. The capacity of the goblet pitcher was estimated as two joined cylinders (small cylinder above large cylinder). The pitcher's contents were removed by suction and the volume of the liquid estimated with a graduated test tube. All contents were put in a petri dish and the numbers of live individuals of each species were counted under a dissecting microscope. Analysis of variance was used to compare and contrast the attributes of the two types of pitchers. Correlation analyses were used to determine the relationship between the pitcher attributes and the abundance of arthropod species.

Ten insects of five different species visiting the pitchers were observed and followed individually for more than 30 min each (2 species of Coleoptera, 2 species of Diptera, and 1 species of Hymenoptera). This permitted us to characterize the pitcher's prey attraction strategy, and the potential factors that may cause the insects to fall into the pitchers.

The larvae living inside the pitchers were collected and reared to the adult stage. Voucher larval and adult specimens were stored in alcohol and then sent out for identification or verification. The dy-

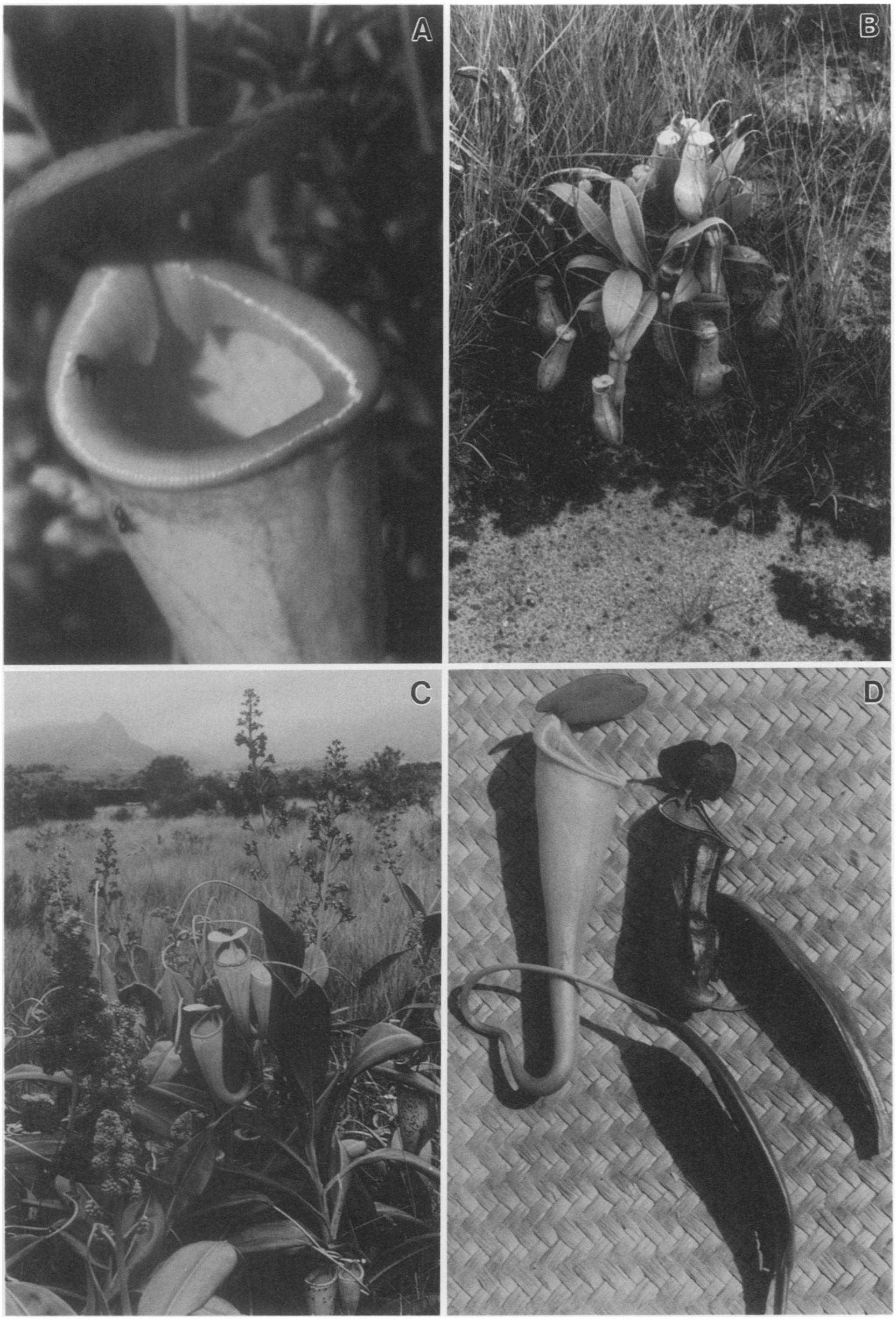

FIGURE 1. (A) Peristome of a trumpet pitcher of *Nepenthes madagascariensis* showing a fly foraging for nectar on the lip and a predatory spider (*Thyena* sp.) just below the lip. (B) micro-habitat for the rosette, goblet form, at the edge of a *Sphagnum* mat. (C) general habitat for *Nepenthes madagascariensis:* the climbing, trumpet form is shown along with inflorescences. (D) close up of pitchers; trumpet form is left, goblet right, both formed at the end of the tendril and leaf blade; colors vary from individual to individual.

TABLE 1. *Comparison of the Goblet and Trumpet pitcher attributes of* Nepenthes madagascariensis.

	Mean		Standard deviation			
	G	T	G	T	*F* value	*P* value
Capacity of pitcher (cm^3)	28.78	41.81	21.34	19.97	10.43	0.0017
Height above ground (m)	0.02	0.74	0.06	0.36	196.16	0.0001
Volume of liquid (ml)	12.65	8.47	7.08	4.11	13.75	0.0003
Number of mosquito larvae (*Uranotaenia belkini*)	5.77	0.00	4.87	0.00	74.17	0.0001
Number of mosquito larvae (*Uranotaenia bosseri*)	0.75	2.06	1.78	3.26	6.44	0.012
Number of mites (*Creutzeria* sp.)	10.46	29.96	9.11	19.48	42.89	0.0001
Number of fly larvae (Chloropidae)	1.38	9.81	1.78	5.41	113.7	0.0001

G: Goblet pitcher; T: Trumpet pitcher.

namics of pitcher colonization were examined by marking each of 15 newly-opened goblet and trumpet pitchers and following arthropod colonization over their lifetime. The number of individuals of each species present was tallied from opening until the death of the pitcher. The contents of the pitcher were removed at each census, as above, and then returned to the pitcher after the numbers of micro-community members were tallied.

To characterize site selection by the egg-laying mosquitoes, a pilot study was done using paper cups filled with water or pitcher fluid. Ten paper cups were filled with water and 10 others with fluid from opened goblet and trumpet pitchers. The paper cups were placed on the ground next to the growing pitchers. After four days, the cups were examined for eggs and larvae.

Food web interactions were established using behavioral observations of micro-community members in the field and laboratory.

RESULTS AND DISCUSSION

Nepenthes spp. pitchers provide a short-lived habitat for many arthropod species (Beaver 1983). *Nepenthes madagascariensis* pitchers were observed to remain functional for about three months (96 ± 8 days, range 80–120 days, sample size 60).

Structurally, *Nepenthes madagascariensis* displays two radically different pitcher forms and associated ecology, depending on the age of the plant. The juvenile, rosette form has short, goblet shaped pitchers, which are borne at ground level and are often partly sunken in the *Sphagnum magellanicum* peat mats with which it is commonly associated (Table 1) (Fig. 1B, D). The adult plant produces long, narrow, trumpet-shaped pitchers, which are borne on climbing stems and are well exposed to visiting insects (see Table 1) (Fig. 1C, D). It takes about nine months on average for a rosette, juvenile plant to mature and begin producing trumpet pitchers (265 ± 20 days, range 220–310, $N = 50$).

Various flying insects (see below) and ants (Formicidae) visit the pitchers and collect the copious nectar secreted (Fig. 1A). In any given visit, an insect may spend 30 min or more consuming nectar on an individual pitcher. The insects seem to become progressively more dizzy over time and, with increasing likelihood, fall into the pitcher. The plant does produce alkaloids and essential oils present in varying amounts in the leaf tissue, nectar and the pitcher fluid. This finding was based on our analysis of samples following the methods outlined by Stermitz *et al.* 1989. The alkaloids may cause disorientation in the prey and increase their probability of falling into the pitcher (pers. obs.). No significant levels of ethanol were detected (*i.e.,* <0.002M) in the nectar or pitcher fluid, using a standard alcohol dehydrogenase assay (Worthington Biochemical Corp. 1993). Finally, in working with the pitchers over a few hours we developed headaches and began to feel dizzy ourselves.

Once the insect visitor falls into the pitcher fluid, it takes only a few seconds for it to become immobilized. Prey type and prey number vary from one pitcher to another. Various insects including Hymenoptera (bees, wasps, ants), Diptera (flies), Coleoptera (beetles), Araneae (spiders), Orthoptera (grasshoppers, crickets) and Lepidoptera (moths, butterflies) form the most common prey in the pitchers.

Although the liquid inside the pitcher appears toxic for most invertebrates, some species actually live inside the pitcher and subsist on the prey captured. These include:

1) Various unidentified microorganisms (bacteria, protozoa, yeast, etc.). These are active decomposers and form important food sources for filter-feeding insects living in the liquid.
2) Mites (*Creutzeria* sp.) are benthic detritivores.

TABLE 2. *Correlations among* Nepenthes *goblet pitcher attributes.*

	Capacity of pitcher	Height above ground	Volume of liquid	Mosquito larvae (*U. belkini*)	Mosquito larvae (*U. bosseri*)	Mites	Fly larvae
Capacity of pitcher	—						
Height above ground	−0.299*	—					
Volume of liquid	0.200	−0.108	—				
Mosquito larvae (*U. belkini*)	0.038	−0.228	0.341*	—			
Mosquito larvae (*U. bosseri*)	0.148	0.008	0.0800	−0.404**	—		
Mites	−0.147	−0.026	0.1540	0.213	−0.029	—	
Fly larvae	−0.234	0.203	−0.0110	0.053	0.000	0.393**	—

* P value < 0.05.
** P value < 0.01.
$N = 52$.

Their colonization and dispersal to and from the pitchers are closely associated (a phoretic association) with a frit fly (Chloropidae) that also colonizes the pitchers. In the absence of other arthropods, mite populations can be quite large. For example, the pitchers of an isolated population of *Nepenthes madagascariensis* with only mites present showed populations of more than 200 mites in many instances. With other arthropods present, the number of mites averaged 60.

3) A species of frit fly commonly occurs in the pitchers. The larvae are found mainly along the upper walls, near the fluid surface. Individual larvae feed on dead or decaying organic matter (carrion feeders), and are attracted to the recently drowned insects.
4) Two species of mosquito larvae live in the pitchers: *Uranotaenia belkini* and *U. bosseri*. *Uranotaenia bosseri* is a filter feeder, and often browses along the surface of recently drowned insects. *Uranotaenia belkini* is both a filter feeder and an aquatic predator. It was observed to grab, kill and consume individuals of *U. bosseri*. Grjebine (1979) had reported four species of mosquitoes occurring in association with this pitcher plant species: *Uranotaenia belkini, U. damasei, U. bosseri* and *U. brunhesi*. *Uranotaenia belkini* and *U. damasei* were reported only from goblet pitchers while *Uranotaenia bosseri* and *U. brunhesi* occurred only in trumpet pitchers (Grjebine 1979). However, we observed only two species of mosquitoes associated with *Nepenthes madagascariensis* at the main study sites and in other populations examined. *Uranotaenia belkini* was found only in goblet pitchers, but *U. bosseri* was associated with both types of pitchers. The two other species of mosquitoes, *U. damasei* and *U. brunhesi,* are apparently quite rare (Grjebine 1979).
5) Several species of spiders were associated with *Nepenthes madagascariensis* pitchers. *Thyena* sp. (Salticidae) constructs a nest under the lip of the peristome, while *Peucetia* sp. (Oxyopidae) and *Theridion decaryi* (Theridiidae) spin webs around the pitcher's mouth. An unidentified crab spider (Thomisidae) can descend on a silk line below the surface of the pitcher's fluid and remain there for several minutes before reemerging. The crab spiders were observed taking fresh insects that had fallen into the liquid, but were never seen preying on the resident mosquito larvae living in the pitcher. The spiders prey not only on insects that visit the pitcher nectaries but also on the resident insects that have emerged as adults from the pitcher fluid.
6) Other occasional terrestrial predators include mantids (*Polyspilota aeruginosa*—Dictyoptera) and dragonflies (Odonata) which prey on insects visiting the pitchers and on resident insects that emerge from the pitcher fluid.
7) Predatory ants (*Tetraponera sahlbergi*—Formicidae) often use the hollow, senescent stems of the pitcher plants as nest sites.
8) Lizards (*Phelsuma* sp.—Geckonidae) were observed to establish territories on groups of pitcher plants and consume not only the insects visiting the pitchers but also the nectar secreted around the pitcher's opening. Tree frogs (*Heterixalus tricolor*—Hyperoliidae) may occupy the pitchers occasionally as temporary shelters.

The attributes of the two pitcher forms are quite different. The overall volumetric capacity of trumpet pitchers was much greater than that of goblet pitch-

TABLE 3. *Correlations among* Nepenthes *trumpet pitcher attributes.*

	Capacity of pitcher	Height above ground	Volume of liquid	Mosquito larvae (*U. bosseri*)	Mites	Fly larvae
Capacity of pitcher	—					
Height above ground	0.199	—				
Volume of liquid	−0.079	−0.249	—			
Mosquito larvae (*U. bosseri*)	0.043	−0.123	0.068	—		
Mites	0.207	0.125	−0.020	0.183	—	
Fly larvae	0.237	0.076	−0.004	−0.323*	0.179	—

* P value < 0.05.
$N = 53$.

ers, but the liquid volume was significantly greater in goblets than in trumpets (Table 1). The lids of goblet pitchers tended to be more open than those of trumpets, so that goblet pitchers may have filled more easily with rainwater. In addition, trumpet pitchers tended to be located in exposed areas where evaporation of the pitcher's liquid may have been more rapid; goblet pitchers were usually located in shaded areas close to ground level. The liquid volume in *Nepenthes madagascariensis* varied from 1–30 ml, compared with means of a few milliliters up to 1 liter in other *Nepenthes* species (Lloyd 1976). The mosquito *Uranotaenia belkini* was found only in the goblet pitchers, while *Uranotaenia bosseri* was more abundant in trumpet pitchers than in goblet pitchers (Table 1). Mites (*Creutzeria* sp.) and frit flies were significantly more numerous in trumpet pitchers than in goblet pitchers (Table 1).

Correlation analyses were used to determine the relationship of the pitcher's attributes to the abundance of micro-community members for each pitcher type. The relationships were quite different in the two forms of pitchers. In goblet pitchers, a significant negative relationship was found between the abundance of the two species of mosquitoes (Table 2). This result probably reflects the observed predatory behavior of *U. belkini* toward *U. bosseri*. A positive relationship was seen between the number of mites (*Creutzeria* spp.) and the frit flies (Table 2), reflecting the phoretic association between them (see below). The abundance of various arthropod species inside the pitchers appeared to be largely independent of the capacity of the pitcher and the height of the pitcher above ground. A positive correlation was seen between the abundance of *Uranotaenia belkini* and the volume of the liquid (Table 2). The significant negative correlation between the capacity of the goblet pitcher and its height from the ground is unclear (Table 2).

In trumpet pitchers (Table 3), there was a negative relationship between the number of mosquitoes (*U. bosseri*) and the frit flies. Both species were observed feeding on or near dead insect parts (saprophagous) and may compete for some of the same resources in this microcosm. *U. bosseri* typically colonizes the pitchers long after the frit flies, which by this time are close to completing their aquatic life cycles. The abundance of the arthropods in trumpet pitchers appeared to be independent of the size of the pitcher, the height of the pitcher above ground and the volume of the pitcher's liquid (Table 3). Chance seems to play an important role in determining which pitchers are colonized by mosquitoes.

Colonization of the pitchers by micro-community arthropods differed in the two forms of pitchers. In goblet pitchers, frit fly eggs were seen on the first day of opening (Figure 2A). Frit fly larvae were first seen between the seventh and the 14th day on average (Figure 2B). Mites and mosquitoes were first observed as larvae (or adults) in the pitcher (Figures 2, C & D). Larvae of *Uranotaenia belkini* were found on average by the second day after opening (Figure 2D). No *Uranotaenia bosseri* larvae were observed in the experimental goblet pitchers. In trumpet pitchers, frit fly eggs were seen on the second day of opening (Figure 3A). Frit fly larvae were visible between the third and the seventh day (Figure 3B). Mites were first observed in trumpet pitchers between the second and the third day after opening (Figure 3C). Colonization of trumpet pitchers by mosquitoes (*Uranotaenia bosseri*) was delayed to between the 30th and the 40th day after pitcher opening (Figure 3D). This delayed colonization may be associated with the suitability of conditions inside the pitcher for the development of mosquito larvae. Sequential changes in the microhabitat may facilitate the colonization by the other species, such as these mos-

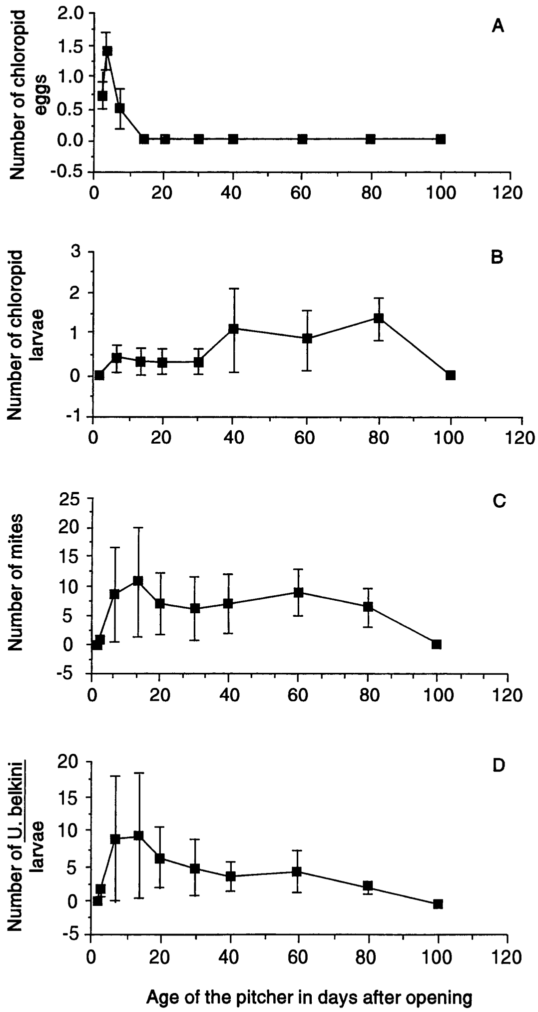

FIGURE 2. Colonization of arthropods in *Nepenthes* Goblet pitchers. Points represent the average number of arthropods observed inside *Nepenthes madagascariensis* goblet pitchers. Horizontal axis shows the age of the pitcher in days after opening. Error bar is 1 ± SD, N = 15. A: Chloropid eggs; B: Chloropid larvae; C: Mites (*Creutzeria* sp.); D: Mosquito larvae (*Uranotaenia belkini*).

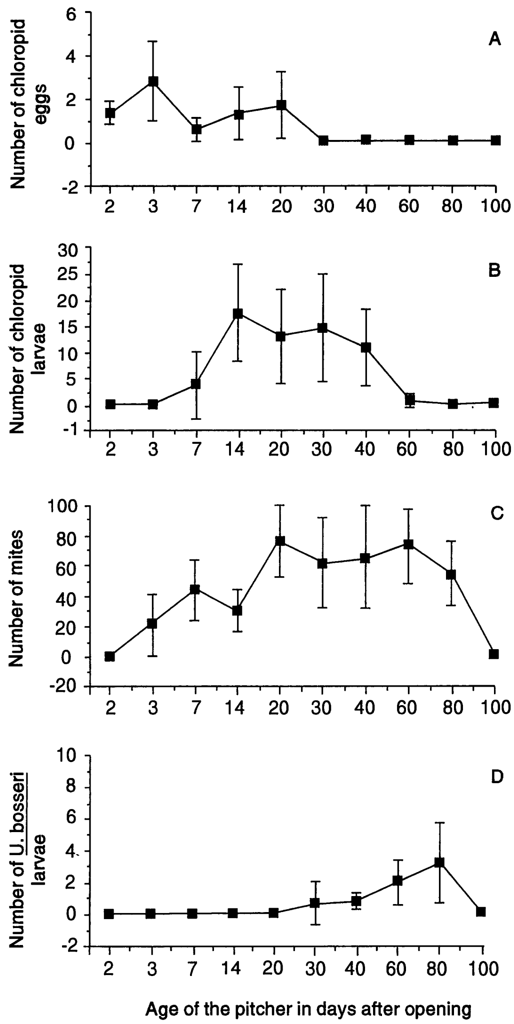

FIGURE 3. Colonization of arthropods in *Nepenthes* Trumpet pitchers. Points represent the average number of arthropods observed inside *Nepenthes madagascariensis* trumpet pitchers. Horizontal axis is the age of the pitcher in days after opening. Error bar is 1 ± SD, N = 15. A: Chloropid eggs; B: Chloropid larvae; C: Mites (*Creutzeria* sp.); D: Mosquito larvae (*Uranotaenia bosseri*).

quitoes. A temporal change in micro-community composition has also been reported for other species of *Nepenthes* (Beaver 1985, Kitching & Beaver 1990). The delayed colonization may also reflect competitive interactions with the frit fly larvae.

Fewer frit flies and mites colonized goblet pitchers than trumpet pitchers. Mites are dispersed by clinging to the thorax of the adult frit flies that emerge from the fluid in both pitcher types. Only two adult frit flies were successfully raised in the laboratory out of more than 100 larva, and both carried out mites on their thorax. Only rarely were terrestrial predators such as the jumping spider (*Thyena* sp.) seen on goblet pitchers, but these were quite common on trumpet pitchers (Fig. 1A). Most trumpet pitchers had but one jumping spider (*Thyena* sp.) present. This species is apparently territorial and it shows aggression toward conspecifics on the same pitcher. Quantitative data on pitcher colonization by spiders were not collected.

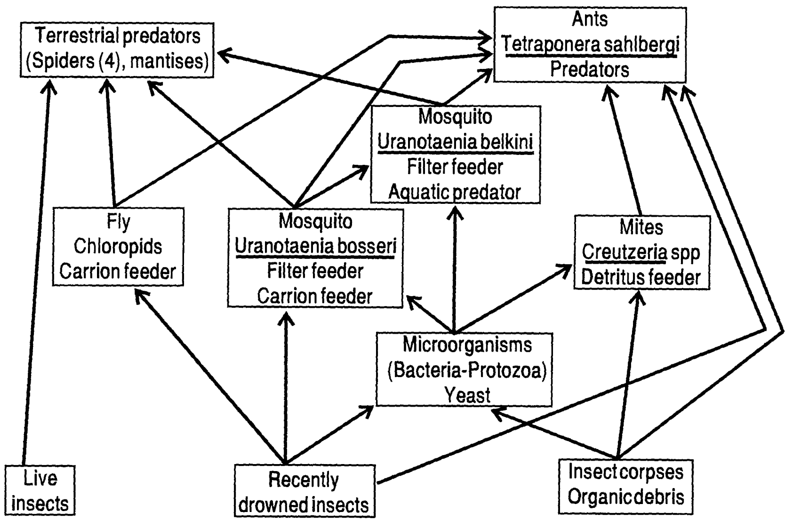

FIGURE 4. Food web interactions in *Nepenthes madagascariensis*. A box represents a species or a trophic component. An arrow from box A to box B means that consumer B feeds on resource A.

Uranotaenia belkini appear to oviposit in the liquid from goblet pitchers regardless of container attributes. *Uranotaenia belkini* accepted the paper cup with fluid from the goblet pitcher (6 out of 10 cups contained *U. belkini* mosquito larvae). The 10 paper cups filled with water were ignored by *U. belkini*. The paper cups filled with the liquid from trumpet pitchers were not selected by any mosquitoes. Oviposition by *Uranotaenia bosseri* may be restricted to pitchers only, or perhaps to sites off the ground. In any case, no *Uranotaenia* species were observed in any water-filled habitat near *N. madagascariensis* populations (*e.g.*, *Ravenala madagascariensis* bracts, *Pandanus* spp. water tanks or other phytotelmata).

Food webs are defined by the feeding interactions between consumers (predators) and resources (prey) (Pimm 1982). A food web of the micro-community associated with *Nepenthes madagascariensis* pitchers is shown in Figure 4. The interactions were obtained from the experimental studies described above as well as from field observations. The communities living inside the pitchers include no important producers. The main source of energy for the organisms living here was the input of prey from outside the system. Some of the insects visiting the pitcher were caught by terrestrial predators: Araneae (spiders), Odonata (dragonflies), Dictyoptera (mantids). Most of the insects that fall into the pitcher drown. Fresh prey in the pitcher are sometimes retrieved and eaten by crab spiders (Thomisidae). Recently drowned insects are fed upon directly by fly larvae and also support bacteria, yeast and protozoan populations. Bacteria, yeast and protozoa are consumed by the filter feeders (*U. belkini* and *U. bosseri*). The mosquito (*Uranotaenia bosseri*) browses across the surfaces of recently drowned insects. The remains of the pitchers' prey accumulate at the bottom of the pitcher, and further organic debris may be added in the form of small pieces of plant material that fall into the pitchers. The organic debris is used by mites, which may also feed on microorganisms living on the debris (Beaver 1983). *Uranotaenia bosseri* is preyed upon by *Uranotaenia belkini*.

Ants (*Tetraponera sahlbergi*, Formicidae) constitute the main predators of the aquatic organisms. These ants access the pitcher's content by making holes in the lower part of the pitchers. The fluid drains and the ants consume the living organisms (mosquitoes, flies, mites) as well as any dead organisms and debris in the pitcher (up to 100% in some populations). Ant predation is quite common, with more than 70 percent of the pitchers drained in some populations. However ant predation is rare in goblet pitchers. Terrestrial predators living on or near the pitchers (spiders, mantids, *etc.*) feed on the living insects visiting the pitcher, as well as upon insects that emerge after completing their life cycle in the pitcher fluid. The food web matrix of *Nepenthes madagascariensis* shown in Table 4 follows Warren & Lawton (1987), in which the entries are either 0 (no interaction) or 1 (predator A preys on resource B).

TABLE 4. *Food web matrix for* Nepenthes madagascariensis.[1]

		Consumer									
		1	2	3	4	5	6	7	8	9	10
Resource	1	0	1	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0	0
	3	0	0	0	1	1	0	0	0	1	1
	4	0	1	0	0	0	0	0	0	0	1
	5	0	0	0	0	0	0	1	1	1	0
	6	0	0	0	0	1	0	1	0	0	1
	7	0	0	0	0	0	0	0	0	0	1
	8	0	1	0	0	0	0	0	0	0	1
	9	0	1	0	0	0	0	0	1	0	1
	10	0	0	0	0	0	0	0	0	0	0

[1] The matrix was constructed following Warren & Lanton 1987, based on experimental studies in petri dishes and field observaations in which the entry is either 0 or 1. Entry "0" refers to no interaction between the two species while entry "1" indicates that consumer A feeds on resource B. 1. Live insects visiting the pitchers; 2. Terrestrial predators living around the pitchers (spiders, mantids, dragonflies); 3. Recently drowned insects; 4. Frit fly larvae (chloropids); 5. Microorganisms (bacteria, protozoa, yeast); 6. Organic debris; 7. Mites (*Creutzeria* spp.); 8. Mosquito larvae (*Uranotaenia belkini*); 9. Mosquito larvae (*Uranotaenia bosseri*); 10. Ants (*Tetraponera sahlbergi*).

Beaver (1985) published a preliminary food web for *Nepenthes madagascariensis* as part of a broad survey of *Nepenthes* spp. We followed his procedures and terminology in characterizing food web interactions. The major differences in the two food webs for *Nepenthes madagascariensis* are the total number of interactions (Table 5) and the number of genera and species of terrestrial predators (Table 6). These differences are explained by the fact that Beaver's (1985) food web for Madagascar pitcher plants (*Nepenthes madagascariensis*) was based on rather meager, systematic surveys of selected invertebrates found living inside the pitchers (Fage 1930, Paulian 1961, Grjebine 1979).

In sum, *Nepenthes madagascariensis* displays two different structural forms and associated ecological differences. The pitcher provides a short-lived habitat (three months) for several arthropod species. A wide variety of insects is attracted to the pitcher, apparently by the color of the pitcher, the nectar secreted around its opening and probably the odor of the pitcher fluid. During nectar feeding, potential prey appear to become disoriented, and with increasing probability fall into the pitcher and drown. The type and abundance of the prey vary from one pitcher to another. Several arthropod species complete their aquatic life cycles inside individual pitchers. Colonization by mosquitoes is different in the two forms of pitchers. *Uranotaenia belkini* colonize the goblet pitchers by the second day of opening, while colonization of *U. bosseri* is delayed until about the 30th day of opening in trumpet pitchers. Mites (*Creutzeria* sp.) and frit fly larvae are visible during the first week of opening in both types of pitchers. Mites show a phoretic association with adult frit flies that emerge from the pitcher fluid. The food web for this micro-community is more complex than that reported by Beaver (1985).

TABLE 6. *Numbers of genera and species in five guilds inhabiting* Nepenthes madagascariensis *pitchers.*

	Number of genera/species present	
	From Beaver (1985)	This study
Detritus-feeders	1/1	1/1
Filter-feeders	1/4	1/2
Carrion-feeders	1/1	2/2
Aquatic predators	0/0	1/1
Terrestrial predators	1/1	7/7

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TABLE 5. *Food web parameters for* Nepenthes madagascariensis.

	From Beaver (1985)	This study
Number of trophic components (s)	8	10
Number of consumer components (m)	5	7
Number of resource components (n)	6	8
Resource/consumer ratio (n/m)	1.2	1.14
Number of basal components (b_s)	3	3
Number of intermediate components (int)	3	5
Number of top components (n_p)	2	2
Number of interactions (L)	10	19

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