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Prey Spectra of Bornean *Nepenthes* Species (Nepenthaceae) in Relation to their Habitat

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ABSTRAK

Kajian terhadap kandungan mangsa periuk 18 spesis Nepenthe*s di Borneo menunjukkan terdapat 17 kumpulan fauna utama. Hasil kajian mendapati periuk lantai dan udara memerangkap kedua-dua fauna rayap dan fauna terbang, pada umumnya periuk lantai memerangkap lebih banyak fauna rayap sementara periuk udara memerangkap lebih banyak fauna terbang. Kandungan jenis mangsa adalah berkorelasi dengan habitat, spesis yang tumbuh pada habitat berbeza dalam satu lokasi yang sama kadangkala menunjukkan kandungan jenis mangsa yang berbeza. Formicidae didapati jenis mangsa yang kerap ditemui dan yang paling melimpah, dan periuk yang dikutip pada altitud bawah daripada 100 m altitud mengandungi bilangan individu semut yang tinggi tetapi bilangannya didapati menurun dengan peningkatan altitud. Walau bagaimanapun, bilangan semut diperangkap dalam setiap periuk adalah berbeza, contohnya bilangan semut yang ditemui dalam periuk* N. rafflesiana *adalah daripada beberapa individu sehingga 700 individu per periuk. Spesis* Nepenthes *tanah tinggi memerangkap pelbagai jenis mangsa berbanding dengan spesis* Nepenthes *tanah pamah. Spektra mangsa yang pelbagai ini menyediakan lebihan makanan kepada pemangsa menghuni periuk, terutama Arachnida, dan ianya didapati kerap ditemui pada spesis tanah tinggi.*

ABSTRACT

Examination of pitcher prey contents of 18 Bornean pitcher plants showed that pitchers attract 17 fauna groups. The upper and lower pitchers trap both flying and creeping fauna but generally the lower pitchers trap more creeping fauna and upper pitchers more flying prey species. Prey composition is generally correlated with habitat; species occupying different habitats in the same locality sometimes show striking differences in prey composition. Formicidae are the most abundant and frequently trapped, and pitchers collected below 100 m altitude contained enormous numbers of ants but their number generally decreased with altitude. However, the number of ants caught per pitcher was variable, e.g. from a few ants to 700 per pitcher in N. rafflesiana. Nepenthes *species growing at high altitudes trapped a broader spectrum of prey than species at lower altitudes. This broad spectrum of prey provides an ample food source for the pitcher-inhabiting predators, particularly Arachnida, which are common in high altitude species.*

INTRODUCTION

Nepenthes species, commonly known as pitcher plants, are tropical carnivorous plants, which generally grow in areas of infertile soil such as in heath forests, swamp forests, forests on ultrabasic soils, and in limestone forests. *Nepenthes burbidgeae, N. kinabaluensis, N. rajah* and *N. villosa* grow on serpentinized ultrabasic rocks and on acid soils on Mt. Kinabalu (Meijer 1965; Mackinnon 1975; Kurata 1976; Kaul 1982). *Nepenthes northiana* (Anderson 1965; Adam *et al.* 1992), *N. clipeata* (Danser 1928; Adam *et al.* 1992) and *N. mapuluensis* (Adam and Wilcock 1990) are endemic to limestone in Borneo. The ability of *Nepenthes* species to thrive on poor soils is largely attributed to their carnivorous habit of trapping prey in the pitchers, which are a modification of the leaf tip.

Nepenthes species display a carnivorous syndrome, i.e. they attract, retain, trap, kill, digest, and absorb useful substances (Juniper 1986).

The pitchers act as pitfall or passive traps (Lloyd 1942), increasing their efficiency by a seductive device (Slack 1980), the secretion of nectar by numerous glands on the under-surface of the lid and the margin of the inner peristome. The effectiveness of the trap is enhanced by the presence of a waxy, slippery surface on the upper half of the inner surface of the pitcher and sharp descending inner peristome teeth. These teeth are very well developed in some species, for example, in *Nepenthes bicalcarata, N. edwardsiana, N. kinabaluensis, N. rafflesiana, N. rajah,* and *N. villosa.* The pitcher wall secretes a digestive fluid containing enzymes and the products of digestion are absorbed by the same glands (Lloyd 1942).

The prey content of pitchers is varied and includes insects like Hymenoptera (including Formicidae), Isoptera, Coleoptera, Plecoptera, and Dermaptera, and other faunal groups such as millipedes, and snails (Jensen 1910; Adam and Wilcock 1994). Pitcher contents of *Nepenthes* from Borneo have not been extensively studied (Spencer 1860; Slack 1980; Phillipps and Lamb 1988). Slack (1980) noted that pitchers, not referring to any particular species, contained digestive bodies of large insects, such as cockroaches and centipedes as well as scorpions, small mammals and reptiles. Spencer (1860) and Phillipps and Lamb (1988), in an extreme case, mentioned a large rat being trapped in pitchers of *Nepenthes rajah.* Jensen (1910) mentioned the horrible odour arising from pitchers loaded with centipedes, cockroaches, butterflies, and scorpions found in *Nepenthes* near Tjibodas, Java.

The objectives of this study were as follows: (1) to investigate the prey spectra in pitchers of 18 Bornean *Nepenthes* species; (2) to correlate their occurrence and abundance with altitude, habitat and pitcher morphology; (3) to investigate the prey-partitioning between upper and lower pitchers of 9 *Nepenthes* species; (4) to study prey-partitioning between 18 *Nepenthes* species occupying the same locality but growing in different habitat types.

MATERIALS AND METHODS

The localities, habitat, altitude, number of pitchers sampled per species for prey pitcher contents and prey partitioning of 18 Bornean *Nepenthes* are listed in Table 1. Prey pitcher contents were sampled 2 weeks after the pitcher opened. The prey found in the pitchers are listed in Table 2. A total of 255 pitchers were sampled, ranging from 4-47 pitchers per species. Eighteen species and nine species were investigated respectively for prey-partitioning between species (Table 3) and between upper and lower pitchers within a species (Tables 4, 5 and 6).

Using a stereo microscope, the intact fauna were carefully separated from the soils and decayed insect debris from each sample and subsequently preserved in 70% alcohol. Prey was identified to class, order, or family level. Keys to the class of Arthropoda or orders of Insecta (Borror *et al.* 1954), and keys to the class and families of British Insecta (Unwin 1981, 1984) were used. The number of individuals of each taxon in each sample was counted and numbered accordingly.

Duplicate specimens were sent to the Sarawak Forest Department Entomology Section and National Institute of Health, Kyoto. Specimens are deposited in Biology Department Museum, Universiti Kebangsaan Malaysia Sabah Campus and Sarawak Forest Entomology Section. Analysis of principal component analysis (PCA) used a computer statistical programme and Sorenson coefficients similarity (CC) were used to determine fauna group similarity between *Nepenthes* species (Mueller-Dombois and Ellenberg 1974; Brower and Zar 1977).

$$CC = \frac{2c}{s1 + s2} \times 100$$

where s1 and s2 are the number of fauna groups in *Nepenthes* species 1 and 2, and c is the number of faunal groups common in both species.

RESULTS

Diversity of Prey

Of the total 690 taxa collected from 255 pitchers of 18 *Nepenthes* species sampled, 53.9% and 1.2% were identified to family and generic level respectively. A total of 6384 individuals were recorded of which 79.5% (5077 individuals) were Formicidae (excluding other Hymenoptera), 8.4% Isoptera, 3.8% Diptera, 2.6% in other miscellaneous groups, 2.0% Coleoptera, 1.2% Hymenoptera; and less than 1% in each of the other 11 groups (Table 2).

The mean number of individuals per pitcher was 25, but varied greatly between species, ranging from 1.7 individuals in *N. bicalcarata* to 168.9 individuals in *N. macrovulgaris.* Eight *Nepenthes* species had a mean less than 10 individuals per

TABLE 1
Locality, altitude and habitat of pitcher prey sampling sites

No	*Nepenthes* species	Locality	Altitude (m)	Habitat	No. pitchers sampled
1	*N. albomarginata*	Weston, Sabah	5-30	HF	16
2	*N. ampullaria*+	Weston, Sabah	5-30	DDF	7
3	*N. bicalcarata****	Weston, Sabah	5	DDF	7
4	*N. gracilis**	Weston, Sabah	5-30	SWF	20
5	*N. rafflesiana****	Weston, Sabah	5-30	HF	16
6	*N. mirabilis**	Telupid, Sabah	150	SV	10
7	*N. hookeriana***	Telupid, Sabah	150	SV	4
8	*N. macrovulgaris**	Mt. Silam, Sabah	520	RC	7
9	*N. sandakanensis**	Mt. Silam, Sabah	700-800	MF	14
10	*N. lowii***	Mt. Mulu, Sarawak	1680	MF	12
11	*N. muluensis**	Mt. Mulu, Sarawak	1800-2300	MF	16
12	*N. tentaculata**	Mt. Mulu, Sarawak	1600-2300	MF	23
13	*N. x alisaputraiana****	Mt. Kinabalu, Sabah	1900-1930	UF	14
14	*N. curtisii***	Mt. Kinabalu, Sabah	1400	SB	6
15	*N. kinabaluensis****	Mt. Kinabalu, Sabah	2850	UF	16
16	*N. rajah****	Mt. Kinabalu, Sabah	1950	UF	10
17	*N. reinwarditiana**	Mt. Kinabalu, Sabah	960	RC	10
18	*N. villosa****	Mt. Kinabalu, Sabah	1600-2300	UF	47

* Inner surface of lower and upper pitcher partly glandular
** Inner surface of upper and lower pitcher wholly glandular, lower pitcher partly glandular
*** Inner surface of upper and lower pitcher wholly glandular
\+ The only known species to have lower pitcher only, wholly glandular
HF Heath forest
SWF Swamp forest
SV Secondary vegetation
MF Mossy forest
RC Roadside clearing
DDF Disturbed dipterocarp forest
UF Forest on ultrabasic soil

TABLE 2
Prey spectra of eight Bornean *Nepenthes* species

Nepenthes species*	Fauna group	1	2	3	4	5	6	7	8	9
(1)	%	0	0	0	0	0	0	0	11.4	0
(1)	No.	0	0	0	0	0	0	0	71	0
(2)	%	0	0	23	0	0	0	0	69.2	0
(2)	No.	0	0	3	0	0	0	0	9	0
(3)	%	0	0	0	0	0	0	0	91.7	0
(3)	No.	0	0	0	0	0	0	0	11	0
(4)	%	1	0	1	0	0	0	5.9	90	0
(4)	No.	4	0	4	0	0	0	24	367	0
(5)	%	0	0	0	0	0	0	1.9	96.2	0
(5)	No.	0	0	0	0	0	0	43	2239	0
(6)	%	0	0	0	0	1.9	0	0	94.5	0
(6)	No.	0	0	0	0	6	0	0	291	0
(7)	%	0	0	0	0	0	0	0	100	0
(7)	No.	0	0	0	0	0	0	0	60	0
(8)	%	0	0	0	0	0	0	0	99.1	0

Table 2 (cont'd)

Nepenthes species*	Fauna group	1	2	3	4	5	6	7	8	9
(8)	No.	0	0	0	0	0	0	0	1171	0
(9)	%	1.9	0	6.2	0	0	0	31	42.5	1
(9)	No.	3	0	10	0	0	0	50	69	2
(10)	%	16.7	0	17	0	0	0	8.3	45.8	0
(10)	No.	4	0	4	0	0	0	2	11	0
(11)	%	0	0	17	0	0	0	23	36.5	0
(11)	No.	0	0	9	0	0	0	12	19	0
(12)	%	7.5	0	20	0	0	3.7	6	41.2	10
(12)	No.	6	0	16	0	0	3	5	33	8
(13)	%	6	0	5	0	0	0	0	77	0
(13)	No.	6	0	5	0	0	0	0	77	0
(14)	%	0	0	0	6.2	1	0	0	84.5	0
(14)	No.	0	0	0	6	1	0	0	81	0
(15)	%	13.8	4	11	0	3	0	57	0	0
(15)	No.	14	4	11	0	3	0	58	0	0
(16)	%	2.5	0	1	0	0	0	5.9	85.5	0
(16)	No.	8	0	4	0	0	0	19	275	0
(17)	%	0	0	3	0	0	0	3.1	81.7	2
(17)	No.	0	0	11	0	0	0	11	293	7
(18)	%	13.4	8	33	1	3	0	9.2	0	0
(18)	No.	22	13	53	2	5	0	15	0	0

Table 2 (cont'd)

Nepenthes species*	Fauna group	10	11	12	13	14	15	16	17	Total	Mean
(1)	%	0	0	86.3	0	0	0	0	2.3	100	-
(1)	No.	0	0	534	0	0	0	0	14	619	38.7
(2)	%	0	0	0	0	7.1	0	0	0	100	-
(2)	No.	0	0	0	0	1	0	0	0	13	1.9
(3)	%	0	0	0	0	8.3	0	0	0	100	-
(3)	No.	0	0	0	0	1	0	0	0	12	1.7
(4)	%	0	0	0	0	0	0	0	1.9	100	-
(4)	No.	0	0	0	0	0	0	0	8	409	20.4
(5)	%	0	0	0	0	0	0	0	1.9	100	-
(5)	No.	0	0	0	0	0	0	0	43	2325	145.3
(6)	%	0	0	0	0	0	0	0	3.6	100	-
(6)	No.	0	0	0	0	0	0	0	11	308	30.8
(7)	%	0	0	0	0	0	0	0	0	100	-
(7)	No.	0	0	0	0	0	0	0	0	60	15.0
(8)	%	0	0	0	0	0	0	0	0.9	100	-
(8)	No.	0	0	0	0	0	0	0	11	1182	168.9
(9)	%	0	16	0	0	0	0	0	1.2	100	-
(9)	No.	0	26	0	0	0	0	0	2	162	11.6
(10)	%	8.3	0	0	0	4.2	0	0	0	100	-
(10)	No.	2	0	0	0	1	0	0	0	24	2.0
(11)	%	0	23	0	0	0	0	0	0	100	-
(11)	No.	0	12	0	0	0	0	0	0	52	3.3
(12)	%	0	6.2	0	0	0	1.3	1.3	2.5	100	-
(12)	No.	0	5	0	0	0	1	3	2	80	3.5
(13)	%	2	0	4	2	2	0	0	2	100	-

Table 2 (cont'd)

Nepenthes species*	Fauna group	10	11	12	13	14	15	16	17	Total	Mean
(13)	No.	2	0	4	2	2	0	0	2	100	7.1
(14)	%	3.1	0	0	3.1	2.1	0	0	0	100	-
(14)	No.	3	0	0	3	2	0	0	0	96	16.0
(15)	%	0	3	0	0	5	0	0	3	100	-
(15)	No.	0	3	0	0	5	0	0	3	104	6.3
(16)	%	0	1.2	0	0	1.2	0	0	2.5	100	-
(16)	No.	0	4	0	0	4	0	0	8	322	32.2
(17)	%	0	6	0	0	0	0	0	3.9	100	-
(17)	No.	0	22	0	0	0	0	0	14	358	35.8
(18)	%	3.1	3.1	0	0	0	0	0	26.4	100	-
(18)	No.	5	5	0	0	0	0	0	43	162	3.5

Key

Fauna group
1 Arachnida
2 Chilopoda
3 Coleoptera
4 Dermaptera
5 Dictyoptera
6 Diplopoda
7 Diptera
8 Formicidae
9 Homoptera
10 Heteroptera
11 Hymenopters (excluding 8)
12 Isoptera
13 Mollusca
14 Orthoptera
15 Plecoptera
16 Pscoptera
17 Others

* *Nepenthes* species numbered as in Table 1

pitcher but two had means of 145.3 (*N. rafflesiana*) and 168.9 (*N. macrovulgaris*). Fifteen prey groups were identified to family level, one prey group each to order and unknown faunal group respectively (Table 2). Six of these prey groups, Formicidae (which excludes other flying hymenopteran taxa), Dictyoptera, Isoptera, Chilopoda, Diplopoda and Mollusca are creeping fauna. The other prey groups are flying insects.

The commonest group was Formicidae, found in abundance in pitchers of 16 *Nepenthes* species. Although the Formicidae were overall the most common group, they were better represented in lowland habitats where they formed 69-100% of pitcher prey in seven of eight species found below 500 m above sea level compared with 3-87% for species growing between 700-2300 m, and they were totally absent from pitchers in *N. villosa* (1600-2300 m) and *N. kinabaluensis* (2850 m).

Diptera were the second most common group although in much lower abundance. In ten of the species studied, they comprised 57% of the prey in pitchers of *N. kinabaluensis*, 31% in *N. sandakanensis*, and 23% in *N. muluensis*. While the pitchers of the remaining seven species contained between 2-9% Diptera. Sixty-five Dipteron taxa were recognized, belonging to families such as Phoridae, Syrphidae, Cecidomyiidae and Sciaridae.

Coleoptera, the third most common prey group encountered, were recorded in ten species, being most abundant in pitchers of *N. villosa* (33%), *N. ampullaria* (23%), *N. tentaculata* (20%), *N. lowii* (17%), *N. muluensis* (17%) and *N. kinabaluensis* (11%). Eighty-two coleopteran taxa were recognized belonging to families such as Curculionidae, Scarabaeidae, Elateridae, Chrysomilidae, Pyrochoridae, Odemeridae, Carabidae, Passalidae, Nitidulidae, Buprestidae, Cerambycidae and Lucanidae.

Hymenoptera (excluding Formicidae) were found in ten species studied, being abundant in *Nepenthes muluensis* (23%) and *N. sandakanensis* (16%). Forty-six Hymenopteran taxa recognized belong to families such as Chacidoidae, Apidae, Vespoidae, Trichgrammatidae and *Icheu monidae*. Hymenopteran species recognized included *Apis cerana* (in *N. muluensis*), *Trigona* sp. (in *N.* x *alisaputraiana*, *N. gracilis*, and *N. rajah*), and *Dacus* sp. (in *N. gracilis*). *Bulbitermis* sp. (Isoptera) were present in abundance in *Nepenthes albomarginata* and comprised 86% of the prey.

The other 12 fauna groups were less common, and each group never comprised more than 10% of the pitcher prey of the 18 species of *Nepenthes* recorded (Table 2).

Fig. 1-3 give the results of principal component analysis (PCA) of the faunal contents of 67 pitchers collected from 18 species from 30-2970 m

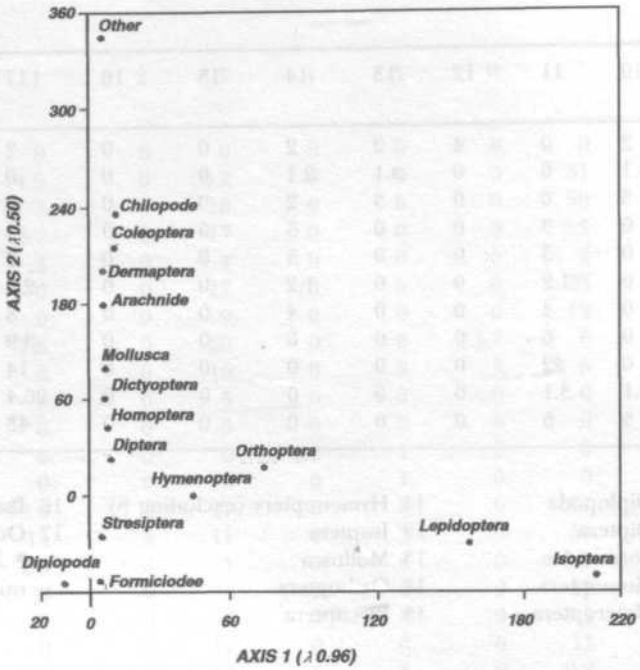

Fig 1. Principal compenent analysis (PCA) of prey type in 18 Bornean Nepenthes

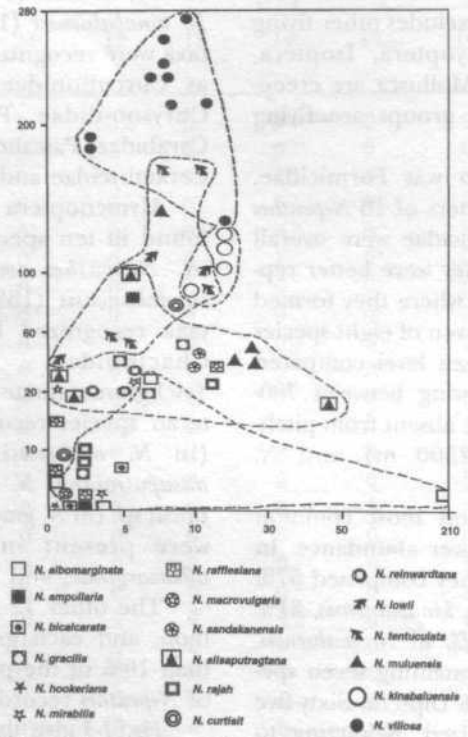

Fig 2. Principal component analysis for 67 pitcher samples from 18 Nepenthes *species*

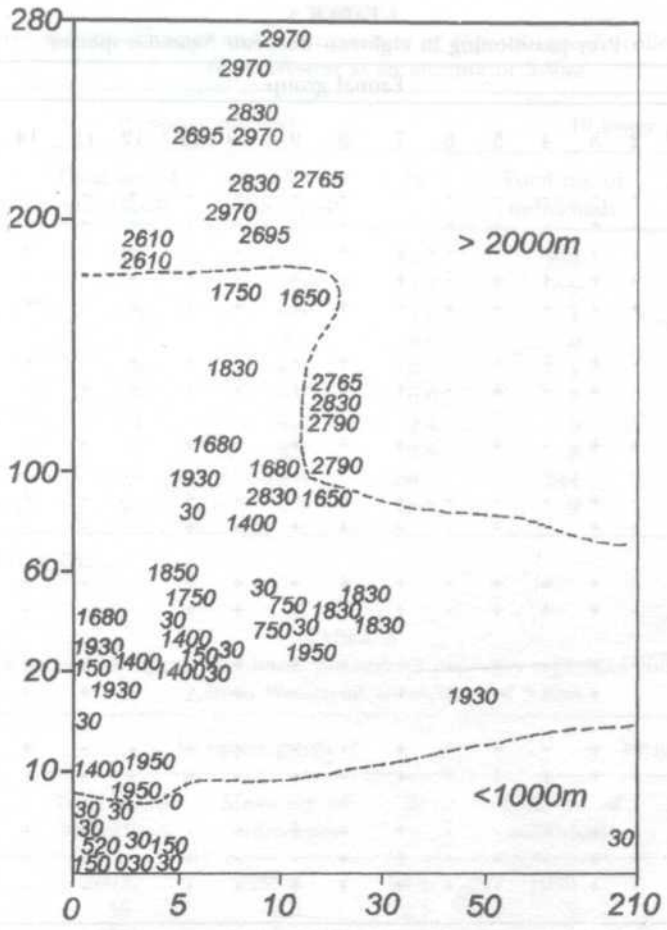

Fig 3. Principal component analysis of Nepenthes *pitcher samples*

above sea level. Apart from the unusual prey composition of *N. albomarginata*, which had an abundance of *Bulbitermis* sp. (Isoptera), the principal variation relates to altitude (*Fig. 3*). *Nepenthes* species at higher altitudes have a greater diversity of fauna prey (Table 1) and *Fig 1* shows that Isoptera and Formicidae are much commoner, while Isoptera and Lepidoptera are confined to low altitudes. Although there is a considerable overlap, some species have fairly distinct prey spectra, particularly those at higher altitudes.

The prey spectra of 18 Bornean *Nepenthes* species studied showed similarity with prey spectra of *N. mirabilis* sampled in New Guinea (Table 3). Sorenson's similarity coefficient (Mueller-Dombois and Ellenberg 1974; Brower and Zar 1977) of the prey spectra between species studied (Table 3) is more than 30% in all species and average 64%. Formicidae (excluding other Hymenopteran), Coleoptera, Diptera and Arachnida are common components of *Nepenthes* prey spectra. They are recorded in 16, 11, 10 and 8 *Nepenthes* species studied (Tables 2, 3).

Partitioning between and within Species

Different *Nepenthes* species often occupy different habitats within a single site (Table 1). For example, in Telupid, *Nepenthes mirabilis* and *N. hookeriana* grow in wetter and drier habitats respectively. The prey composition of these two species shows differences, although two of the eight faunal groups (Coleoptera and Formicidae) recorded are present in both species and calculated Sorenson's similarity coefficient value between them is 36% (Table 3). *Nepenthes sandakanensis* and *N. macrovulgaris* collected from mossy forest and roadside clear-

TABLE 3
Prey partitioning in eighteen Bornean *Nepenthes* species

	Faunal group																	
Localities/Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	CC(%)
Weston																		
N. albomarginata	+	-	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	
N. ampullaria	-	-	+	-	-	-	-	+	-	-	-	-	-	+	-	-	-	
N. bicalcarata	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-	
N. gracilis	+	-	+	+	+	-	+	+	+	-	+	-	-	-	-	-	-	37
N. rafflesiana	+	+	-	-	-	+	+	+	+	+	+	-	-	+	-	-	+	
Telupid																		
N. hookeriana	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	
N. mirabilis	+	-	+	-	+	-	+	+	+	-	-	-	+	-	-	-	+	36
PNG																		
N. mirabilis	+	+	+	-	+	-	+	+	+	+	+	-	+	-	-	-	-	
Mt. Silam																		
N. macrovulgaris	-	-	+	-	-	-	+	+	-	-	+	-	-	+	-	-	+	
N. sandakanensis	+	+	+	-	-	-	+	+	+	-	+	-	-	-	-	-	-	61
Mamut																		
N. curtisii	-	-	+	+	+	-	+	+	+	+	+	-	-	+	-	-	+	
N. reinwardtiana	+	-	+	+	+	-	+	+	+	+	+	-	-	-	-	-	-	94
Pig Hill																		
N. x alisaputraiana	+	-	+	-	+	-	+	+	+	+	-	-	+	+	+	-	-	
N. rajah	+	-	+	-	+	+	+	+	-	+	-	-	+	-	-	-	+	73
Mt. Kinabalu																		
N. kinabaluensis	+	+	+	-	+	+	+	-	-	-	+	-	-	+	-	-	-	
N. villosa	+	+	+	+	+	+	+	-	+	+	+	+	-	-	-	-	-	74
Mt. Mulu																		
N. lowii	+	-	+	-	-	-	+	+	+	+	-	-	-	+	-	-	-	
N. muluensis	+	-	+	-	-	-	+	+	-	-	+	-	-	-	-	-	-	74
N. tentaculata	+	-	+	-	-	+	+	+	+	+	+	-	-	-	-	-	-	

+ - present – absent CC= Sorenson coefficient similarity (refer to method)
PNG - Papua New Guinea (Jebb 1989)
Key to faunal group: refer in TABLE 1

ing respectively on Mt. Silam in Lahad Datu, Sabah provides another example. Four of the nine faunal groups (Coleoptera, Diptera, Formicidae and Hymenoptera) were found in both species.

However, several species pairs found on the same site and occupying the same habitat show markedly similarly prey composition (Tables 1, 3), namely *N. reinwardtiana* and *N. curtisii* collected from a roadside clearing or secondary vegetation at Mamut, *N. rajah* and *N. x alisaputraiana* growing in mossy forest on Mt. Kinabalu, and *N. villosa* and *N. kinabaluensis* occupying gnarled forest on ultrabasic soil on the summit trail of Mt. Kinabalu. Full analysis of prey-partitioning was not possible because no sampled *Nepenthes* was common to more than one site.

Comparison between upper and lower pitchers in *Nepenthes gracilis* (Table 4) and *N. rafflesiana* (Table 5) show that flying taxa are more numerous in upper pitchers. However, the principal prey in both species are ants and in *N. rafflesiana* these are more numerous in the lower pitchers than the upper pitchers. Similar comparisons between upper and lower pitchers of *Nepenthes* species are summarized in Table 6. Six of these seven species (except *Nepenthes tentaculata*) contained higher mean numbers of individuals of crawling taxa in the lower pitchers than in the upper pitchers.

DISCUSSION

This study of 18 *Nepenthes* species shows that they possess various characters which may act as an attractant to potential prey. All the 18 species

TABLE 4
Prey spectra of upper and lower pitchers of *Nepenthes gracilis* collected from Weston at an altitude of 5-30m

Faunal group	10 upper pitchers			10 lower pitchers		
	Total no. of individuals	Mean no. of individuals	%	Total no. of individuals	Mean no. of individuals	%
Formicidae*	134	13.4	80.7	232	23.2	95.2
Diptera+	22	2.2	13.2	5	0.5	2.1
Coleoptera+	3	0.3	1.8	1	0.1	0.4
Dermaptera+	1	0.1	0.6	0	0	0
Homoptera+	0	0	0	1	0.1	0.4
Hymenoptera+	1	0.1	0.6	2	0.2	0.8
Dictyoptera+	4	0.4	2.4	0	0	0
Arachnida*	1	0.1	0.6	3	0.3	1.2
Total	166	16.6	100	244	24.4	100
Total no. of flying fauna	27	2.7	16.3	9	0.9	3.7

*creeping Insects; + flying fauna

TABLE 5
Prey spectra of upper and lower pitchers of *Nepenthes rafflesiana* collected from Weston at an altitude of 5-30m

Faunal group	10 upper pitchers			10 lower pitchers		
	Total no. of individuals	Mean no. of individuals	%	Total no. of individuals	Mean no. of individuals	%
Formicidae+	2003	250.4	94.4	1036	129.5	98.8
Diptera*	39	4.9	3.1	5	0.6	0.5
Orthoptera+	10	1.3	0.8	0	0	0
Coleoptera+	10	1.3	0.8	1	0.13	0.09
Lepidoptera+	2	0.3	0.2	1	0.13	0.09
Homoptera	2	0.3	0.2	1	0.13	0.09
Diplura+	2	0.3	0.2	0	0	0
Hymenoptera+	1	0.1	0.1	2	0.25	0.19
Arachnida*	5	0.6	0.4	2	0.25	0.19
Chilopoda	1	0.1	0.1	1	0.13	0.09
Total	2075	259.4	100	1049	131.1	100
Total of flying fauna	66	8.3	3.2	10	1.25	1.0

*creeping Insects; + flying fauna

studied produced both upper and lower pitchers, which, however, display varying shapes and colours. The shapes of the pitcher ranged from tubulose (*N. x alisaputraiana* and *N. rajah*; *Plate 1A and 1D*), infundibulate (*N. kinabaluensis*; *Plate 1B*), infundibulate-globose (*N. lowii*; *Plate 1C*) tubulose-ventricose, infundibulate-ventricose, ovate, globose and urceolate; and the colour of the pitchers ranges from green with mottling purple, green, dark red or scarlet to yellowish-red. It has been suggested by Lloyd (1942), Heslop-Harrison (1978); Joel (1984, 1988) that the various pattern of pitcher shapes and bright colouring are among the common mechanisms to attract potential prey. Joel (1988) reported that the pitchers of the same *Nepenthes* species are conspicuous to insects due to the overall shining colour, such as scarlet or golden yellow in *N. bicalcarata*, or deep red as in *N. ampullaria*. The pitcher is a seductive, alluring or attractive device; insects are attracted by the nectar secreted by the glands covering the inner surface

TABLE 6
Prey spectra of lower and upper pitchers of seven Bornean *Nepenthes* species

Nepenthes species	Pitcher	No. of pitchers	Mean no. of individuals per pitcher		
			flying taxa	crawling taxa	Total
N. albomarginata	Upper	10	1.0	6.4	7.4
	Lower	6	0.2	90.6	90.8
N. kinabaluensis	Upper	10	4.6	1.6	6.2
	Lower	6	5.3	1.7	7.0
N. lowii	Upper	8	0.6	1.1	1.7
	Lower	4	1.0	1.5	2.5
N. mirabilis	Upper	7	0.7	7.7	8.4
	Lower	3	1.3	81.6	82.9
N. muluensis	Upper	10	2.3	0.5	2.8
	Lower	6	1.5	2.3	3.8
N. rajah	Upper	5	4.8	24.5	29.3
	Lower	5	0.8	34.4	35.2
N. tentaculata	Upper	12	1.3	2.8	4.1
	Lower	12	1.5	1.3	2.8

of the lid (*Plate 2A-F*) and inner peristome margin (*Plate 3A-F*). In this study, 17 of the 18 species studied had numerous nectar glands covering the underside of the lid.

Jebb (1989) suggested a certain degree of prey partitioning between the upper and lower pitchers of the same species. This study shows that the upper pitchers trap enormous numbers of ants, comparable to the number of ants caught by the lower pitchers. A possible explanation is related to the behaviour of the ants. Ants in the tropics nest on shrubs or small trees, and they often move from the nesting site to the ground level. The upper and lower pitchers, particularly of *N. gracilis* and *N. rafflesiana*, are located within the vertical foraging zone of ants and can thus potentially trap enormous numbers. Such a trapping phenomenon is called by Juniper *et al.* (1989) episodic capture of prey. Such an episodic capture of *Bulbitermis* sp. (Isoptera) was observed in a single lower pitcher of *N. albomarginata* from Weston.

Jenzen (1977) suggested that in lowland tropical habitats, ants are omnipresent visitors, guardians, and sugar collectors at most sugar-source floral nectaries, hymenopteran exudates, broken fruits, etc. Hotta (1989) suggested that mossy forest at high altitudes is too moist throughout the year to offer good habitats for ants. This study demonstrates that ants are the main prey component in pitchers of the lowland *Nepenthes* species, decreasing in number with increasing altitude and totally absent in species found in mossy forest located at very high altitudes.

CONCLUSION

This study of fauna pitcher contents of 18 Bornean *Nepenthes* species shows that the pitchers attracted a broad spectrum of prey, which included 17 fauna groups. The upper and lower pitchers trap both flying and creeping fauna, and lower pitchers trap more creeping prey and upper pitchers more flying fauna. The prey composition is correlated with locality; and the species occupying different habitats of the same locality sometimes show striking differences. Formicidae or ants (excluding other Hymenopteran) are the most abundant and frequent prey trapped. The pitcher contents below 100 m altitude contained enormous numbers of ants, generally decreasing in number with increasing altitude; no ants were caught in pitchers of *N. villosa* collected at 1600-2300 m altitude, and pitchers of *N. kinabaluensis* at 2850 m altitude.

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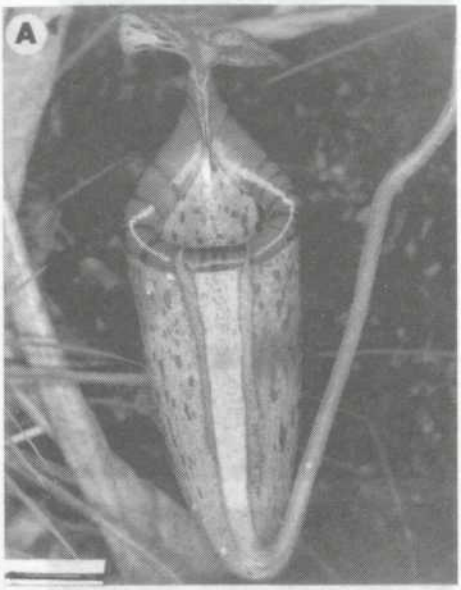

Plate 1A. Lower pitcher of Nepenthes x alisaputraiana
Scale bar 4 cm

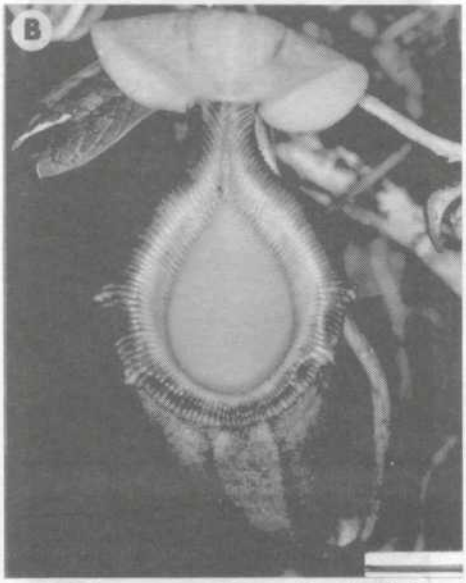

Plate 1B. Upper pitcher of Nepenthes kinabaluensis
Scale bar 6 cm

Plate 1C. Upper pitcher of Nepenthes lowii
Scale bar 6 cm

Plate 1D. Ground pitcher of Nepenthes rajah
Scale bar 8 cm

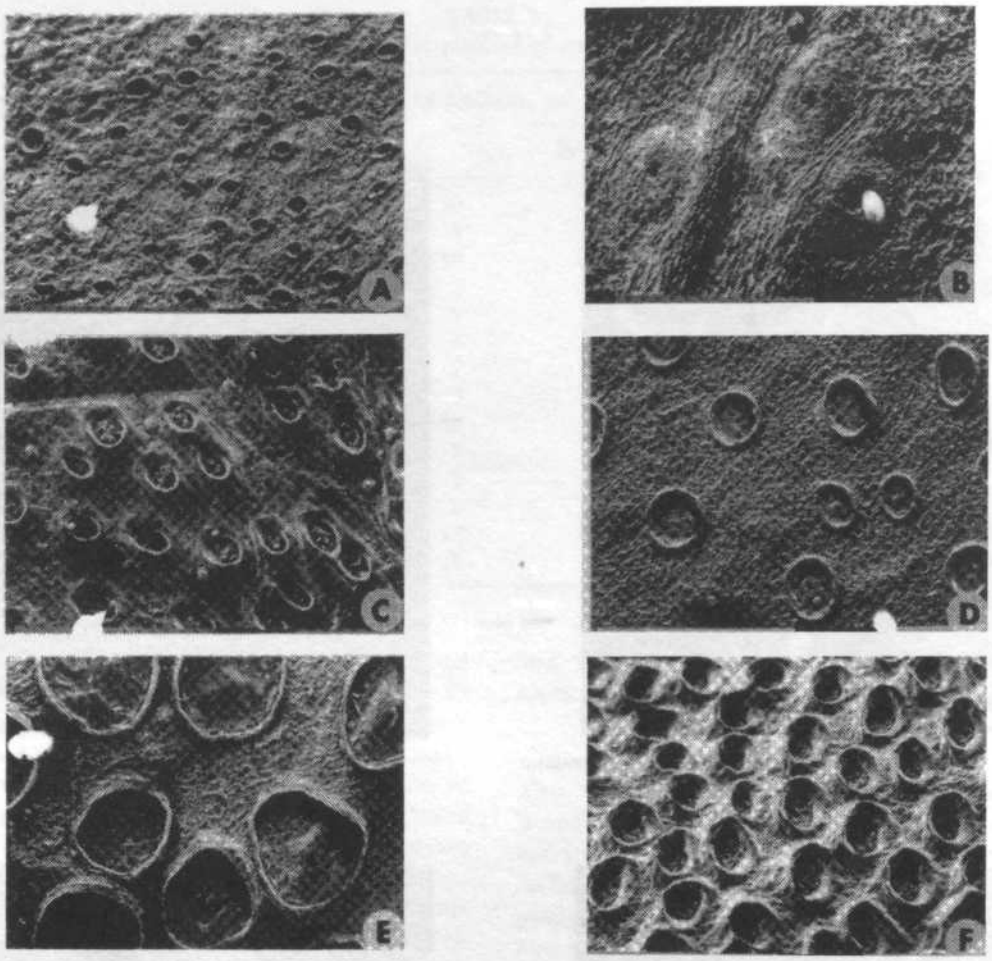

Plate 2A. Lid nectar glands of Nepenthes albomarginata *Scale Bar 400 μm*
Plate 2B. Lid nectar glands of Nepenthes gracilis *Scale Bar 400 μm*
Plate 2C. Lid nectar glands of Nepenthes kinabaluensis *Scale Bar 400 μm*
Plate 2D. Lid nectar glands of Nepenthes mirabilis *Scale Bar 400 μm*
Plate 2E. Lid nectar glands of Nepenthes rafflesiana *Scale Bar 400 μm*
Plate 2F. Lid nectar glands of Nepenthes villosa *Scale Bar 400 μm*

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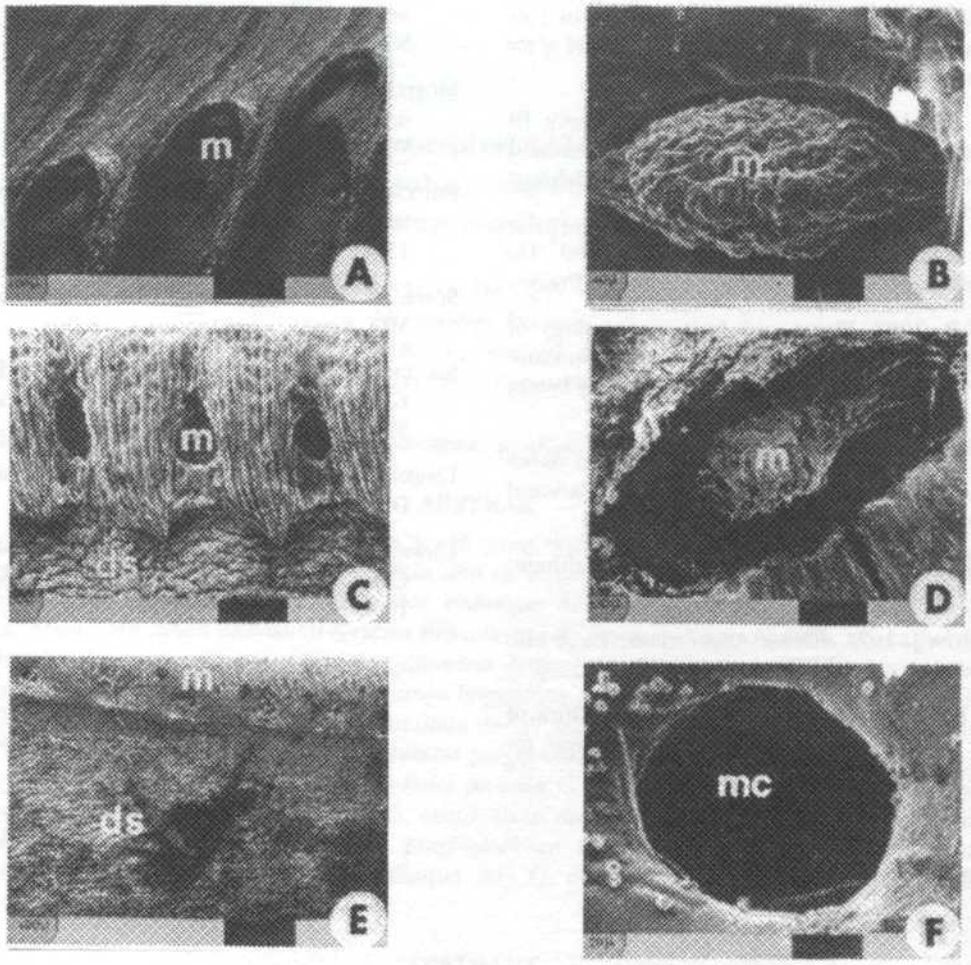

Plate 3A. Marginal glands (m) of Nepenthes rafflesiana *Scale bar 400 μm*
Plate 3B. Marginal glands (m) of Nepenthes rafflesiana *Scale bar 40 μm*
Plate 3C. Marginal glands (m) of Nepenthes gracilis *Scale bar 200 μm*
Plate 3D. Marginal glands (m) of Nepenthes rajah *Scale bar 100 μm*
Plate 3E. Marginal glands (m) of Nepenthes reinwardtiana *Scale bar 400 μm*
Plate 3F. Marginal gland cavity (mc) of Nepenthes reinwardtiana *Scale bar 20 μm*

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