



Aspects of Pitcher Morphology and Spectral Characteristics of Six Bornean *Nepenthes* Pitcher Plant Species: Implications for Prey Capture

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Pitcher plants of the genus *Nepenthes* attract and trap invertebrate prey using nectar-secreting pitchers. Pitcher morphology and spectral reflectance characteristics were investigated for six *Nepenthes* species from northwest Borneo (*N. albomarginata*, *N. ampullaria*, *N. bicalcarata*, *N. gracilis*, *N. mirabilis* var. *echinostoma* and *N. rafflesiana*). Morphological measurements focused on the size of the pitcher rim (or peristome, the site of the major nectaries) in relation to pitcher length. The results show considerable interspecific variation in morphology. Spectral reflectance measurements quantified the degree of colour contrast between the peristome and pitcher body, from ultraviolet (UV) to red wavelengths. The contrast maxima for each species were compared with insect visual sensitivity maxima. The six species showed a wide range of reflectance patterns, with pitchers of *N. rafflesiana* possessing the greatest degree of 'fit' between contrast maxima and insect sensitivity maxima, in the UV, blue and green regions of the spectrum. Based on the morphological and reflectance analyses, we hypothesized that pitchers of *N. rafflesiana* would be more attractive to anthophilous (flower-visiting) invertebrates than the sympatric *N. gracilis*. Analysis of prey contents generally supported the hypothesis, suggesting possible interspecific resource partitioning. Morphological and spectral characteristics of the other species are discussed in relation to published studies on prey capture by those species.

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INTRODUCTION

Colour patterns are used by many angiosperm species to guide anthophilous (flower-visiting) insects to the optimal sites for pollen transfer (Jones and Buchmann, 1974; Kevan, 1986; Menzel and Shmida, 1993; Chittka, 1996). The attraction of anthophilous insects to high-contrast ultraviolet (UV) patterns is also exploited by some predatory species to entice prey. For example, Craig and Bernard (1990) report such patterns in the webs of spiders in Panama. High-contrast UV patterns have also been identified in the trapping structures of several carnivorous plant genera (Joel, Juniper and Dafni, 1985). Two studies have shown UV patterning in Old World pitcher plants of the family Nepenthaceae: Glossner (1992) identified a high-contrast UV pattern in a pitcher of *Nepenthes alata* Blanco, and Moran (1996) demonstrated the presence of UV patterns on the pitchers of *Nepenthes rafflesiana* Jack in Borneo. In *N. rafflesiana* the rim of the pitcher mouth, or peristome (which contains the main nectaries of the pitcher and is the site of primary interest to most visiting invertebrates), is UV-absorptive and stands out in contrast to other areas of the pitcher, which are reflective. Insects are attracted to the peristome by a combination of this visual pattern and a sweet fragrance produced by the fluid within the pitcher. The peristome appears to offer a secure foothold for most visiting invertebrates (Moran, pers. obs.). However, in order

to gain better access to the nectaries on its lower inside edges, some individuals will stray onto the slippery inner wall of the pitcher and eventually fall into the digestive fluid and drown.

In this study we extend the investigation of pitcher colour patterns, within the UV and visible wavebands, to five other Bornean lowland *Nepenthes* species as well as *N. rafflesiana*. The study comprised three components: (1) to describe the spectral characteristics of the pitchers, specifically the degree of colour contrast between peristome and pitcher body; (2) to characterize morphology of aerial pitchers of each species, in terms of peristome size relative to the pitcher body; and (3) to use the results of the first two parts of the study to make predictions about the relative attractiveness of two sympatric species to anthophilous prey. The null hypothesis was that the prey spectra of the two species would be identical, despite interspecific differences in pitcher characteristics.

MATERIALS AND METHODS

Species investigated

Six Bornean lowland species were surveyed: *Nepenthes albomarginata* Lobb; *N. ampullaria* Jack; *N. bicalcarata* Hook. f.; *N. gracilis* Korth.; *N. mirabilis* var. *echinostoma* Druce; and *N. rafflesiana*. Pitchers were collected from areas of degraded heath, freshwater swamp and peat swamp forests between the towns of Gadong and Seria in Brunei,

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northwest Borneo (4° 34' N, 114° 25' E). *Nepenthes* plants produce dimorphic pitcher types, known as aerial and terrestrial, which differ in their placement relative to the ground, as well as in their morphology (Juniper, Robins and Joel, 1989; Clarke, 1997). Only aerial pitchers were used in this study since previous studies had demonstrated their enhanced attraction for flying prey over terrestrial pitchers (Jebb, 1991; Moran, 1996). The one exception was *N. ampullaria*, for which terrestrial pitchers were investigated, since aerial pitchers are rarely produced and are of such a small size and vestigial nature that their value to the plant as invertebrate traps is doubtful (Green and Green, 1964; Clarke and Moran, 1994).

Pitcher measurements

Ten mature and fully-developed pitchers of each species were collected, each pitcher being taken from a separate plant. Two morphological measurements were made per pitcher: (1) total pitcher length, defined as the vertical distance between the 'hook' at the rear of the pitcher lid, and the lowest part of the pitcher body, at the point of tendril attachment; and (2) the width of the peristome was measured on either the left or the right side of the pitcher, using slide calipers.

Spectral analysis

After morphological measurements were taken, spectral reflectance analysis was carried out on the ten pitchers of each species, to determine the degree of colour contrast between peristome and pitcher body. Each pitcher was scanned twice for reflected radiant flux ($\text{W m}^{-2} \text{nm}^{-1}$), from 350 nm (UV) to 700 nm (red) at 2 nm intervals, in indirect natural light, using a LI 1800 spectroradiometer with an 1800-06 Microscope Receptor/UV Quartz Microscope attachment (Li-Cor Inc., Lincoln, NE, USA). The first reading was taken from the peristome, the second from an area of the pitcher body directly below and adjacent to it. For each pitcher, both readings were taken within a few minutes of each other, to counter temporal effects on the spectrum of incident light. From this data, a measure of contrast (C) between peristome and pitcher body at each 2 nm step was derived using the formula of Dusenbery (1992):

$$C = \frac{I_p - I_b}{I_b}$$

where I_p and I_b are the mean reflected radiant flux values ($\text{W m}^{-2} \text{nm}^{-1}$) for peristome and pitcher body, respectively, at a given wavelength.

Reflectance data from the spectroradiometer scans showed a tendency towards high noise: signal ratios at UV wavelengths ($< 400 \text{ nm}$). To counter this and elucidate the underlying trends, peristome: body contrast data were smoothed using the LOWESS (locally weighted regression) algorithm, applying a tension value of 0.1 (Wilkinson, 1990). Accuracy of the relative reflectances in the UV range produced by the smoothing process, was verified with UV photography of the pitchers using a Kodak 18A

filter (Eastman Kodak Co., Rochester, NY, USA), which was transmissive between 300 and 390 nm, but visually opaque, allowing UV contrast patterns to be compared.

Prey sampling from sympatric populations of *N. rafflesiana* and *N. gracilis*

To test if interspecific differences in pitcher characteristics would result in a difference in prey composition, the prey contents of two species, *N. rafflesiana* and *N. gracilis*, were compared. The species were chosen for two reasons. Firstly, they occur sympatrically, often in very close proximity, and are thus exposed to an identical range of potential prey species. Secondly, their pitchers possess different morphological and colour characteristics (see Results and Discussion). Based on these differences, we predicted that *N. rafflesiana* would be more successful than *N. gracilis* at trapping potentially anthophilous invertebrate prey. Thirty aerial pitchers of each species (one per plant) were collected from a strip of degraded coastal heath forest where both species occurred sympatrically, and their prey contents counted and classified as far as possible using a dissecting microscope. In most cases, prey items were represented by exoskeletal remains only.

All data were analysed using SYSTAT v. 5.05 and SigmaStat v. 2.0 (SPSS Inc., Chicago, IL, USA). Frequencies of prey capture were compared between *N. rafflesiana* and *N. gracilis* using Chi-square (χ^2) tests. Since the tests used one degree of freedom, Yates' correction factor was applied to reduce the risk of type I errors (Sokal and Rohlf, 1981).

RESULTS AND DISCUSSION

Pitcher measurements

Data are presented as box plots (Fig. 1). Total pitcher lengths showed the following trend in size: *N. mirabilis* $>$ *N. rafflesiana* $>$ *N. bicalcarata* $>$ *N. albobmarginata* $>$ *N. gracilis* $>$ *N. ampullaria* (Fig. 1A). The width of the peristome in each species (Fig. 1B) showed the trend *N. mirabilis* $>$ *N. rafflesiana* $>$ *N. ampullaria* $>$ *N. bicalcarata* $>$ *N. albobmarginata* $>$ *N. gracilis*. The peristome:body ratio, calculated by dividing the peristome width value by pitcher length value for each pitcher (Fig. 1C), provides an index of peristome size in relation to pitcher size. Results showed the following trend: *N. ampullaria* $>$ *N. mirabilis* $>$ *N. rafflesiana* $>$ *N. bicalcarata* $>$ *N. albobmarginata* $>$ *N. gracilis*, i.e. in relation to their length, the pitchers of *N. ampullaria* have the widest peristome, those of *N. gracilis* the narrowest.

Spectral analysis

Figure 2 shows the mean reflected energy ($\text{W m}^{-2} \text{nm}^{-1}$) from the peristome and pitcher body of the six species ($n = 10$ per species) over the waveband 350–700 nm. The thin lines in Fig. 3 denote the reflectance contrast between peristome and pitcher body. Negative contrast values indicate that the peristome is darker than the pitcher body at that wavelength; positive values denote the opposite. We

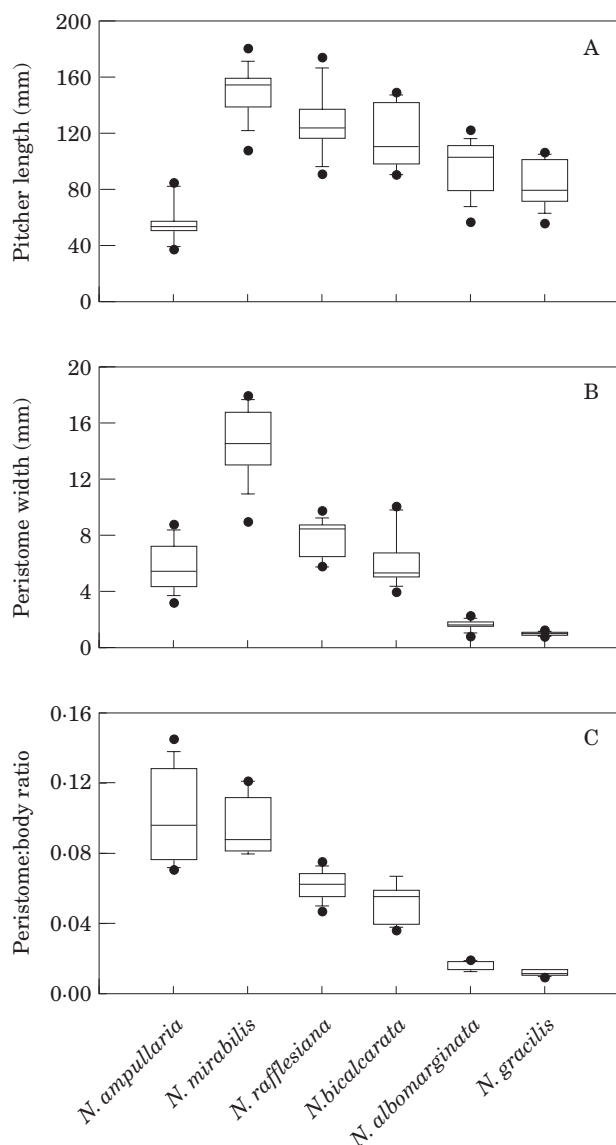


FIG. 1. Box plots of pitcher measurements for the six *Nepenthes* species studied. Upper and lower boundaries of the box denote the 75th and 25th percentiles, respectively, horizontal line within the box marks the median. Upper and lower bars represent the 90th and 10th percentiles, respectively. Outliers are represented by closed circles. $n = 10$ for each species. A, Pitcher length (mm); B, width of peristome (mm); C, Peristome:body ratio, derived by dividing the peristome width by pitcher length.

refer to both peaks (positive) and troughs (negative) in reflectance contrast as contrast maxima, since they are in effect opposite but equivalent. Trichromatic sensitivity maxima for several insect orders (Hymenoptera, Orthoptera, Hemiptera, Odonata, Blattoptera, Diptera, Lepidoptera; Peitsch *et al.*, 1992; Chittka and Menzel, 1992) are denoted as thick lines in Fig. 3 and correspond to ultraviolet (UV) (λ 330–370 nm; only part of the range ≥ 350 nm is given in Fig. 3), blue (B) (λ 430–470 nm) and green (G) wavebands (λ 490–540 nm). Although there is evidence for sensitivity to red in some insect groups (e.g. Coleoptera; Dafni *et al.*,

1990), this waveband generally appears to be less important than those of shorter wavelengths (Peitsch *et al.*, 1992; Proctor, Yeo and Lack, 1996).

There was a broad range of reflectance contrast patterns between peristome and pitcher body amongst the six species surveyed. *N. rafflesiana* possessed perhaps the most complex pattern, with three discrete peristome:body contrast maxima: -0.55 at 374 nm (UV); 0.48 at 480 nm (blue); and 0.85 at 670 nm (red), i.e. the peristome was less than half as reflective as the body in the UV part of the spectrum, but more reflective in the blue and red bands (Figs 2A and 3A). There was considerable correspondence, or 'fit', between peristome:body contrast maxima and all three insect visual sensitivity maxima (UV, B and G, Fig. 3A) in this species. (Note: there is an error in Table 3 of Moran (1996), in which reported reflectance values from peristome and body of *N. rafflesiana* at 440 nm are reversed, and reported body reflectance measurements are too large by a factor of ten. For example, the mean values for reflectance from aerial pitchers at this wavelength should read 0.073 and 0.056 for peristome and body, respectively). *N. gracilis* showed a much less complex pattern (Figs 2B and 3B), with a noticeable contrast maximum of 0.38 – 0.36 in the waveband 350–352 nm (UV) only, i.e. the peristome was about one third more reflective than the pitcher body in this part of the UV. Thus, there was correspondence between contrast maxima and insect visual sensitivity maxima in the UV, but not the blue or green regions (Fig. 3B). *N. bicalcarata* (Figs 2C and 3C) showed no contrast maximum in the UV, but small maxima of -0.17 at 450 nm (violet), 0.32 at 548 nm (green) and -0.16 at 668 nm (red). There appeared to be some correspondence between contrast maxima and insect visual sensitivity maxima in the green and blue regions only (Fig. 3C). The peristome of *N. ampullaria* was less reflective than the pitcher body across the whole of the waveband analysed, with contrast values ranging from -0.40 (violet/UV) to -0.28 (green) (Figs 2D and 3D). There was little or no correspondence between the distribution of contrast maxima and insect sensitivity maxima in the green and blue regions only (Fig. 3E). *N. albomarginata* showed the opposite reflectance pattern: a consistently more reflective peristome over the waveband analysed, with a contrast maximum of 1.0 at 520 nm (green) (Figs 2F and 3F). There was a high degree of correspondence between a contrast maximum and an insect visual sensitivity maximum in the green region (Fig. 3F).

Comparison of prey composition in *N. rafflesiana* and *N. gracilis*

Pitchers of *N. rafflesiana* caught more individual prey items in all taxa than those of *N. gracilis* (Table 1). Since the prey contents of the pitchers represented the total number of

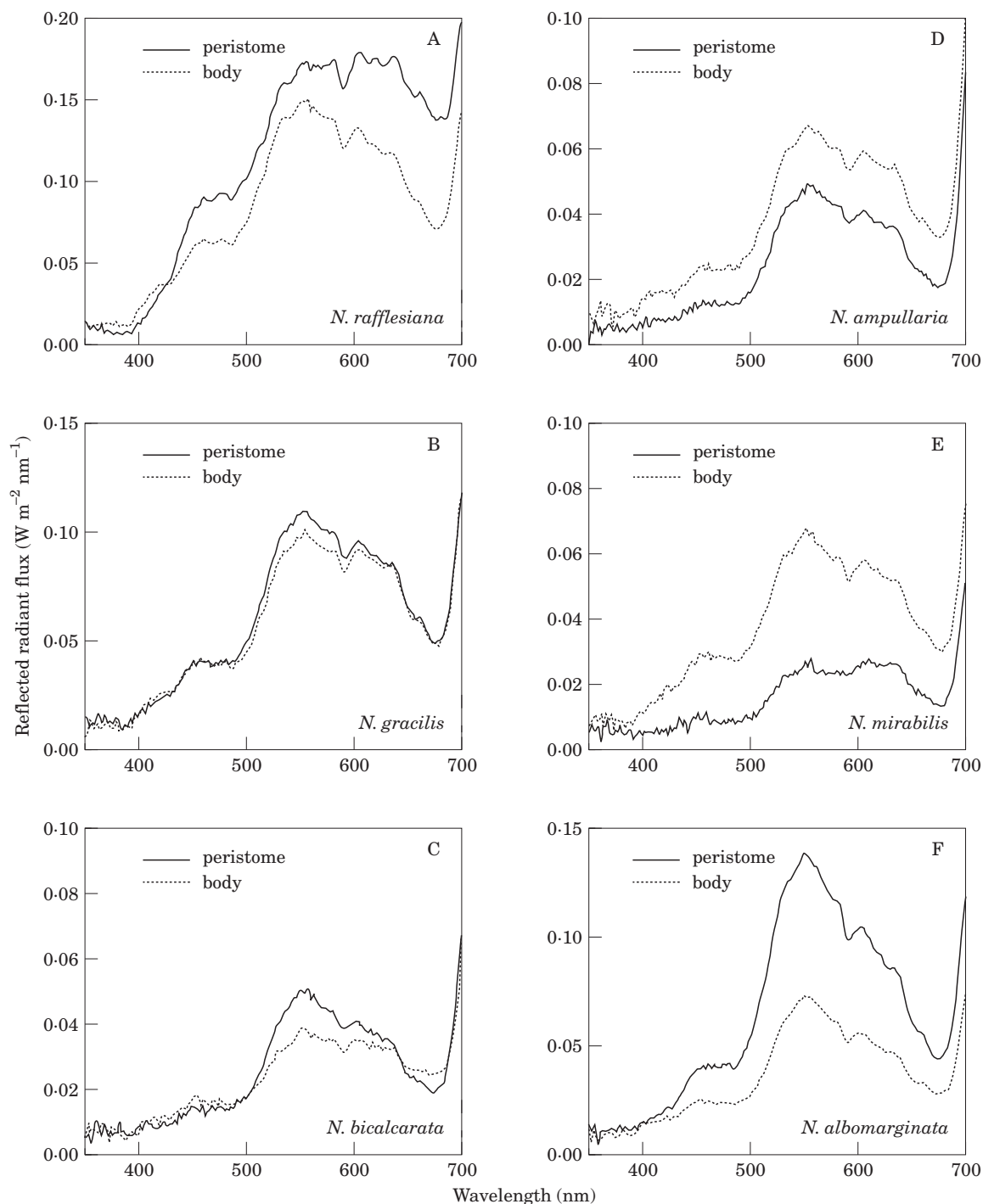


FIG. 2. Reflectance characteristics of pitchers of *N. rafflesiana* (A), *N. gracilis* (B), *N. bicalcarata* (C), *N. ampullaria* (D), *N. mirabilis* (E) and *N. albomarginata* (F). Lines show mean values ($n = 10$) for reflected radiant energy ($\text{W m}^{-2} \text{nm}^{-1}$) from peristome (—) and pitcher body (···) in the waveband 350–700 nm, in indirect natural light.

prey items caught over the life of the pitcher up until the time of sampling, we took the conservative view that any differences in total prey number are due solely to interspecific differences in functional lifespan of the pitchers. Therefore, comparison of the frequencies of prey taxa between the two species was carried out using Chi-square (χ^2) tests. Expected

frequencies were calculated from the ratio of total prey items caught between the two *Nepenthes* species. If the difference between two species in the number of prey items in a given taxon is due solely to differences in pitcher lifespan, we would expect the same interspecific proportions for that taxon as are found for total prey numbers. If,

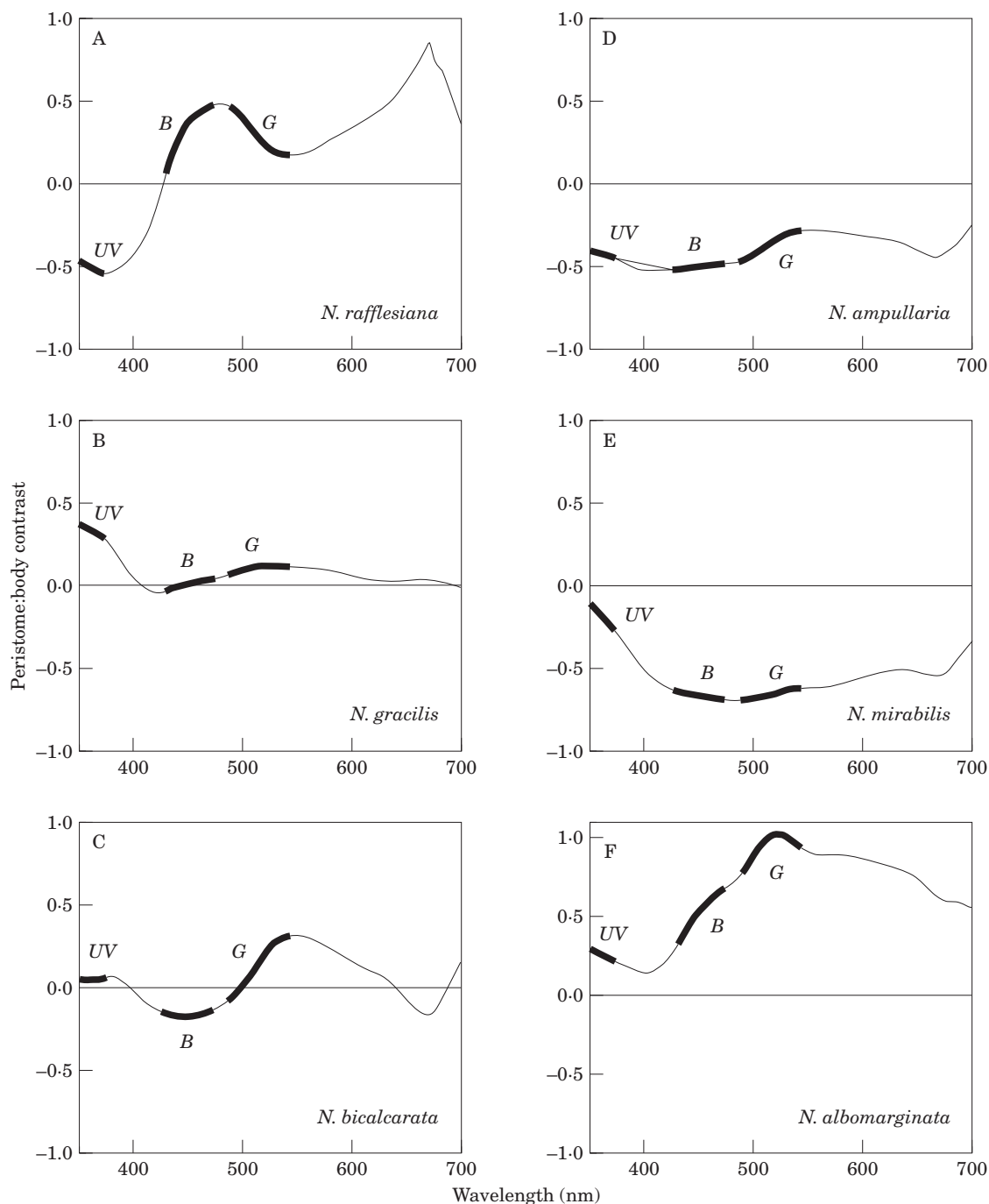


FIG. 3. Peristome:body contrast values for pitchers of *N. rafflesiana* (A), *N. gracilis* (B), *N. bicalcarata* (C), *N. ampullaria* (D), *N. mirabilis* (E) and *N. albomarginata* (F). Contrast was derived using the following formula: $C = (I_p - I_b)/I_b$ where C is the contrast value (no units; $\text{W m}^{-2} \text{nm}^{-1}/\text{W m}^{-2} \text{nm}^{-1}$) and I_p and I_b are the mean reflected radiant flux values ($\text{W m}^{-2} \text{nm}^{-1}$) for peristome and pitcher body, respectively, at a given wavelength (Dusenbery, 1992). Thick lines denote regions corresponding to insect trichromatic sensitivity maxima in the ultraviolet (UV), blue (B) and green (G) wavebands.

however, the proportions are significantly different to those predicted by the overall prey numbers, we can conclude that there is a significant interspecific difference in attraction for, and capture of, that taxon. For example, the ratio of mean number of total prey captured between pitchers of *N. rafflesiana* and *N. gracilis* was 83.5 to 23.5, or 3.5:1. By

contrast, comparison of the mean number of Apidae captured showed a ratio of 3.0 to 0.2, or 15:1, which was shown to be significant at $P < 0.001$ using the χ^2 test (Table 1). Similarly, *N. rafflesiana* pitchers contained significantly more Lepidoptera (moths), Diptera, Thysanoptera and total flying prey than expected, whereas *N. gracilis* pitchers

TABLE 1. Comparison of prey composition and aerial pitcher characteristics between sympatric *N. rafflesiana* and *N. gracilis*

Category	<i>N. rafflesiana</i>		<i>N. gracilis</i>		χ^2	<i>P</i>	Species in which proportion is higher than expected
	Mean (\pm s.e.)	% of total	Mean (\pm s.e.)	% of total			
Hymenoptera-Apidae	3.0 (\pm 0.6)	3.6	0.2 (\pm 0.1)	0.8	14.96	< 0.001	<i>N. rafflesiana</i>
Hymenoptera-wasps	2.0 (\pm 0.5)	2.4	0.8 (\pm 0.2)	3.4	1.77	ns	—
Lepidoptera-moths	3.3 (\pm 0.5)	3.9	0.3 (\pm 0.1)	1.1	13.69	< 0.001	<i>N. rafflesiana</i>
Diptera	17.5 (\pm 3.5)	20.9	2.3 (\pm 0.4)	9.6	40.24	< 0.001	<i>N. rafflesiana</i>
Coleoptera	4.9 (\pm 0.6)	5.9	2.8 (\pm 0.8)	11.7	24.68	< 0.001	<i>N. gracilis</i>
Hemiptera	0.9 (\pm 0.2)	1.1	0.5 (\pm 0.2)	2.3	4.66	0.03	<i>N. gracilis</i>
Thysanoptera	8.4 (\pm 4.1)	10.0	0.0 (\pm 0.0)	0.0	72.43	< 0.001	<i>N. rafflesiana</i>
Total flying prey	40.4 (\pm 7.9)	48.4	6.9 (\pm 1.0)	29.3	48.09	< 0.001	<i>N. rafflesiana</i>
Hymenoptera-Formicidae	42.2 (\pm 9.1)	50.5	16.0 (\pm 3.9)	67.9	27.87	< 0.001	<i>N. gracilis</i>
Araneae	0.7 (\pm 0.1)	0.8	0.1 (\pm 0.1)	0.4	1.47	ns	—
Total flightless prey	43.1 (\pm 9.1)	51.6	16.6 (\pm 3.9)	70.7	32.77	< 0.001	<i>N. gracilis</i>
Total prey	83.5 (\pm 13.4)	100.0	23.5 (\pm 4.3)	100.0	—	—	—
Pitcher length (cm)	13.2 (\pm 0.2)	—	9.5 (\pm 0.2)	—	—	< 0.001†	—
Pitcher elevation (cm)	87.9 (\pm 7.0)	—	103.8 (\pm 5.3)	—	—	ns†	—

Proportions of prey types compared using Chi-square (χ^2) tests; pitcher characteristics compared using *t*-test. *n* = 30 for each species.

† *t*-test used.

ns, Not significant, i.e. *P* > 0.05.

contained significantly more Coleoptera, Hemiptera, formicine Hymenoptera (ants) and total flightless prey than expected.

Influence of pitcher characteristics on prey capture

The results of the study revealed a wide range of pitcher morphology and spectral reflectance characteristics within the six species investigated. Could this diversity be related functionally to a diversity of prey types? To test this, we compared the prey contents of *N. rafflesiana* and *N. gracilis*, two species which commonly occur sympatrically in Borneo, and which were shown to possess differing pitcher characteristics. We concentrated primarily on characteristics of the peristome, since this is the area of greatest nectar supply and is the zone from which potential prey animals proceed into the pitcher, to be trapped. We suggest that there are two main components to the conspicuousness of the peristome. The first is its physical size (in this case, width) in comparison to the overall size of the pitcher. Even in insects such as non-formicine Hymenoptera which possess sophisticated visual systems, visual acuity may be an order of magnitude less than that of a human observer (Kevan and Baker, 1983), and so the wider the peristome, the more likely it is to be noticed by a foraging insect. The second is the degree to which its colour contrasts with that of the pitcher body itself. The aerial pitchers of *N. rafflesiana* possess a highly conspicuous peristome for two reasons. Firstly, in terms of absolute size (as measured by its width), the peristome of *N. rafflesiana* was the second largest after *N. mirabilis*; the peristome: body size ratio was the third highest after *N. ampullaria* and *N. mirabilis*. Secondly, *N. rafflesiana* showed a complex contrast pattern between peristome and pitcher body, which was found to correspond to insect sensitivity maxima in the UV, blue and green regions of the spectrum. The peristome of *N. gracilis* is much less conspicuous by

comparison. As well as having both the narrowest peristome (mean width was almost eight times less than that of *N. rafflesiana*) and the lowest peristome: body ratio overall among the species studied (mean ratio six times less than that of *N. rafflesiana*), the reflectance contrast pattern shows a much weaker correspondence to insect visual sensitivity maxima. Whereas at the peak of UV contrast in *N. rafflesiana* the pitcher body is more than twice as reflective as the peristome (a difference of > 100%), in *N. gracilis* the peristome is more reflective than the pitcher body by only 30%. There are two other notable differences in aerial pitcher characteristics between the two species. Firstly, the pitchers of *N. rafflesiana* are longer than those of *N. gracilis*, by a factor of about 1.5. Secondly, and more importantly for prey attraction (Moran, 1996), the aerial pitchers of *N. rafflesiana* produce a sweet fragrance, whereas those of *N. gracilis* do not. Based on these differences in pitcher characteristics, we predicted that the aerial pitchers of *N. rafflesiana* would be relatively more successful than those of *N. gracilis* in attracting potentially anthophilous insects. The results of the prey analysis confirmed this prediction for the most part: *N. rafflesiana* is more successful at attracting and trapping Apidae, Lepidoptera (moths), Diptera and Thysanoptera, as well as total numbers of flying prey. This result corresponds well with earlier results concerning the prey spectrum of this species in Borneo (Moran, 1996). In comparison to *N. rafflesiana*, *N. gracilis* appears to have a tendency towards specialization in Coleoptera and Hemiptera. This is surprising, as previous studies have shown the importance of fragrance in the attraction of some Coleoptera to flowers (Proctor *et al.*, 1996), and the pitchers of *N. gracilis* are not fragrant. Further study will be necessary to elucidate the mechanism of attraction of the Coleoptera species caught by *N. gracilis*.

Is resource partitioning occurring between the two species? The phenomenon has been reported for sympatric species of other carnivorous plant genera: Karlsson *et al.*

(1987) described prey partitioning among three *Pinguicula* species in Sweden and Thum (1986) reported partitioning by two *Drosera* species in Germany. For the Nepenthaceae, Kato *et al.* (1993) provided evidence of its occurrence between three montane species from Sumatra. In the current study it is important to bear in mind that for both *N. rafflesiana* and *N. gracilis*, formicine Hymenoptera (ants) are overwhelmingly the dominant prey taxon, and there appear to be sufficient numbers in the habitat for both species to utilize. Resource partitioning requires interspecific competition for the resource, which was not demonstrated in this study. A possible candidate for partitioning in the habitat studied is the order Thysanoptera: *N. rafflesiana* averaged 8.4 per pitcher, whilst those of *N. gracilis* contained none at all. Thysanoptera have been shown to respond to both visual and olfactory floral cues (Kirk, 1984, 1985). In all other prey groups which could be identified, representatives were found in the pitchers of both species. However, the relative numbers of Apidae, Lepidoptera (moths) and Diptera caught between the two species might suggest a tendency towards partitioning, although further investigation into the degree of competition between the two species for these prey groups would need to be undertaken before any firm conclusions could be drawn.

Non-formicine Hymenoptera possess probably the most sophisticated visual systems among the insects (Faegri and Van der Pijl, 1980; Peitsch *et al.*, 1992; Chittka *et al.*, 1994), and so the preference of Apidae for pitchers of *N. rafflesiana*, whose reflectance contrast patterns appear to be 'tuned' to the visual sensitivity maxima of Hymenoptera (and other insect groups), is perhaps not surprising. Similarly, many Diptera possess colour vision (Proctor *et al.*, 1996). In addition, many respond to olfactory cues, so based on the differences in pitcher characteristics between the two species, the observed attraction of *N. rafflesiana* for members of this group might be expected. Although visual cues cannot be ruled out completely (Brantjes, 1978; White *et al.*, 1994; Proctor *et al.*, 1996), the enhanced attraction of *N. rafflesiana* for Lepidoptera (moths) can probably largely be accounted for by the fragrance of the pitchers, since the majority of moths caught were nocturnal Pyralidae. There are areas in Brunei and other parts of Borneo where three or more of the *Nepenthes* species used in the current study may be found growing together. Prey comparisons from such multi-species sympatric populations could yield further useful data on the possibility of resource partitioning.

How do pitcher characteristics relate to prey capture in the other species used in the current study? (Because of the variety of habitats occupied by these species, the range of available prey is also likely to be varied, and any interspecific comparisons must be viewed with this in mind.) A recent account of the prey contents of *N. ampullaria* in Brunei (Cresswell, 1998) showed it to be an indifferent carnivore. Over 50% of the necromass found within pitchers was botanical in origin; of the animal remains, formicine Hymenoptera and Isoptera were the dominant components, and potentially anthophilous prey were apparently absent. How does this finding relate to the pitcher characteristics determined in the current study? *N. ampullaria* has the highest peristome:body size ratio among the six species

studied (Fig. 1C), which should contribute to its conspicuousness. Further, there was consistently high reflectance contrast between peristome and pitcher body throughout the waveband analysed (Fig. 3D). However, there was no evidence of any 'fit' of reflectance contrast maxima to insect visual sensitivity maxima (c.f. *N. rafflesiana*, Fig. 3A). This suggests that high contrast between peristome and pitcher body alone is insufficient to produce a functional visual signal, and that the tightness of 'fit' between contrast maxima and insect visual sensitivity maxima, as in *N. rafflesiana*, may be an important component of the visual attraction system. A possible reason for the lack of anthophilous prey in the pitchers of *N. ampullaria* might be that since the pitchers studied by Cresswell (1998) were of the terrestrial form, they were probably positioned on or near to the ground, where they would have been potentially less accessible to flying prey. However, Moran (1996) demonstrated that pitcher height above ground alone has little effect on capture of flying prey: aerial pitchers of *N. rafflesiana*, placed artificially at ground level, caught similar numbers to those positioned above them.

Both Kato *et al.* (1993) and Clarke (1997) reported the predominance of Isoptera in the prey contents of *N. albomarginata* in Sumatra and Borneo, respectively, suggesting a degree of prey specialization. The presence of a tomentose band of tissue immediately beneath the peristome in this species may be of significance in their attraction. Anthophilous insects were not a significant component of the prey contents. The current study showed strong contrast maxima in the blue and green wavebands, with the latter showing close 'fit' to the insect visual sensitivity maximum. Contrast was much less in the UV region (Fig. 3F). As Chittka *et al.* (1994) pointed out, UV is only one component waveband within what is often a polychromatic visual system, and should not necessarily be analysed in isolation. Nonetheless, contrast patterns in the UV probably carry more functional weight as orientation cues than those at longer wavelengths for many insects, since visual sensitivity appears to be negatively correlated with wavelength, and even insects which are deuteranopic, or colour blind, can often distinguish in the UV waveband (Kevan and Baker, 1983). The low degree of reflectance contrast in the UV, combined with the fact that the peristome in this species is narrow and inconspicuous compared to the other species (with the exception of *N. gracilis*, Fig. 1), may account for the low numbers of anthophilous prey reported for this species.

Although two studies provide accounts of the prey spectrum of *N. mirabilis* (Jebb, 1991 for Papua New Guinea; Kato *et al.*, 1993 for Sumatra), neither can be used to make conclusions about functional aspects of pitcher characteristics in Brunei, where the species is represented by an unusual local variant, *N. mirabilis* var. *echinostoma* (Clarke, 1997). The pitchers of this variant possess a peristome much wider, and presumably more conspicuous, than that of other forms found throughout the species' range.

No detailed analysis of the prey of *N. bicalcarata* has yet been published. Based on our analysis of pitcher characteristics (one of the lower peristome:body size ratios among

the six species, concordance of large peristome:body contrast maxima and insect sensitivity maxima only in the green waveband, a lack of strong sweet fragrance) we make the tentative prediction that aerial pitchers of this species are likely to be far less successful at catching anthophilous prey than those of *N. rafflesiana* in the same habitat.

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