Carnivorous Nepenthes pitcher plants are a rich food source for a diverse vertebrate community

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ABSTRACT

Carnivorous pitcher plants capture insect prey to acquire essential nutrients while growing on extremely poor soils. A few individual species have evolved mutualistic relationships with small mammals that visit the traps to harvest nectar, and in return leave faecal droppings in the pitchers. Here we report that a diverse guild of nectar-harvesting vertebrates visits pitchers of two common lowland Nepenthes species without providing any obvious benefit for the plants. Over four consecutive field seasons, we observed four species of sunbirds and one species of tree shrew drinking nectar from pitcher plants. Foraging activity was highest in the morning and late afternoon. Van Hasselt’s, Brown-throated and olive-backed sunbirds were regular and highly abundant pitcher visitors in two different field sites. A crimson sunbird and a lesser tree shrew were each observed harvesting nectar on one occasion. The vertebrates harvested nectar from the pitcher rim (peristome) of N. rafflesiana and from the underside of the pitcher lid of N. gracilis. A comparison of the nectar production of these and three further sympatric species revealed exceptionally high quantities of nectar for N. rafflesiana. Other factors such as plant and pitcher abundance and the habitat preferences of the observed vertebrates are likely to also play a role in their choice to visit particular species. This is the first account of a case of obvious nectar robbing from Nepenthes pitchers by a guild of species that are too large to serve as prey, while the pitcher size and shape prevent faecal droppings from reaching the pitcher’s inside. This interaction provides an example of a possible starting point for the evolution of the elaborate mutualistic relationships observed in some species. Follow-up adaptations of pitcher shape could enable the plants to catch the droppings of their visitors and turn an exploitative relationship into a mutualism.

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Introduction

Asian pitcher plants (genus Nepenthes) are a highly diverse group of carnivorous plants distributed across the Malay Archipelago, with outlying species reaching as far as Madagascar in the west and New Caledonia in the east. The plants use cup-shaped
pitfall traps (pitchers) lined with slippery surfaces to capture, drown and digest insect prey in order to thrive on extremely nutrient-poor soils. The pitcher, anatomically a transformed leaf, consists of a hollow main body, a collar-shaped upper rim (peristome) and a roof-like lid (Figure 1a). Most species exhibit a noticeable dimorphism between pitchers produced by young rosette plants (‘ground pitchers’) and those growing on mature, climbing vines (‘aerial pitchers’). Insects are attracted to the pitcher peristome by means of conspicuous colouration and sweet scent, and are rewarded with sugary nectar which is secreted at the inner peristome edge. The peristome surface is characterised by an intricate micro-pattern which, in most species, renders it highly wettable. While the surface is safe for insects to walk on when dry, it turns extremely slippery when it is wetted by rain or condensation (Bohn and Federle 2004; Bauer et al. 2008).

While most Nepenthes trap insects, some species have recently been shown to engage in mutualistic relationships with vertebrates (Clarke et al. 2009; Grafe et al. 2011; Greenwood et al. 2011). In these exceptional cases, the plant has evolved specific adaptations to attract small mammals. The plant provides food or shelter and in turn collects the nutrient-rich faeces of the animals. In all cases where mutualistic relationships with vertebrates have been demonstrated, the pitchers of the respective plant species have been considerably modified to accommodate the needs of the vertebrate partner. Woolly Bats (Kerivoula hardwickii) regularly roost inside the pitchers of N. hemsleyana in the lowland heath forests of Brunei Darussalam. The pitchers have an elongated tubular pitcher body (Figure 1b) and an unusually low fluid level. This, together with a stable microclimate, makes them an ideal roosting space for the small bats (Grafe et al. 2011; Schöner et al. 2013).

Nepenthes lowii, a Bornean highland species that attracts tree shrews (Tupaia montana), has evolved large, sturdy, widely funnel-shaped pitchers with a backward-bent lid (Figure 1c). A unique jelly-like white secretion on the inside of the lid attracts the tree shrews which have to position themselves above the pitcher opening in order to reach this delicacy (Clarke et al. 2009). Birds such as Mountain Blackeyes (Chlorocharis emiliae) have also occasionally been observed feeding on the N. lowii lid secretion (Phillipps et al. 2008). Nepenthes rajah, another species from the high mountains of Sabah that reportedly attracts tree shrews (T. montana) and summit rats (Rattus baluensis) and captures their faeces (Greenwood et al. 2011; Wells et al. 2011), shows similar adaptations of its pitcher morphology (Figure 1d). The size and shape of the pitcher opening has been shown to be strongly correlated with the body size of the tree shrews (Chin et al. 2010). Like in N. lowii, the lid is bent backwards to allow easy access to the nectaries on its inside while forcing the animal into a position where its droppings are likely to end up in the pitcher.

These observations have raised questions about the possible evolutionary pathways leading to such elaborate adaptations on the plant side. However, without any intermediate forms known between the ‘normal’, carnivorous and the derived, mutualistic lifestyle, the answers to these questions can be speculative at best. Were pitchers pre-adapted by chance to accommodate the vertebrate mutualist? At least in the case of N. lowii, where the mature plant’s pitchers have lost the ability to trap insects and rely entirely on the intake of tree shrew faeces, a complete pre-adaptation seems unlikely. A partial pre-adaptation that encourages vertebrates to
visit, followed by a selection for pitcher traits that allow the plant to take advantage of these visitors, is more easily conceived. For instance, a pitcher could secrete sufficient quantities of nectar to be attractive to nectarivorous vertebrates but might not be adapted to capture the faeces of its vertebrate visitors. An anecdotal record of a sunbird feeding on the nectar of a *N. faizaliana* pitcher (Clarke and Moran 1997) suggests that these birds do at least occasionally include pitcher nectar in their diet.

Here we present a first account of a diverse vertebrate guild harvesting nectar from two common lowland pitcher plant species in Brunei Darussalam which possess no obvious morphological adaptations to capture the faeces of their visitors. The species, *N. rafflesiana* (Figure 1a) and *N. gracilis*, produce pitchers with ‘typical’ morphology that are very effective insect traps (Bauer et al. 2008, 2012, 2015) and produce large quantities of concentrated nectar to attract their prey (Bauer et al. 2009; Merbach 2001; Merbach et al. 2001). In order to test

**Figure 1.** (a) A typical *Nepenthes* trap (here *N. rafflesiana*) consists of a fluid-filled pitcher body (B), a collar-shaped peristome (P) and a roof-like lid (L). Insects are attracted by nectar secreted onto the peristome, and fall into the trap where they drown and are digested by the plant. This ‘standard’ trap design has been considerably modified in species that engage in mutualistic relationships with mammals: the pitchers of *N. hemsleyana* (b) are elongated and contain only very little fluid, making them a preferred daytime roost for woolly bats. (c) *N. lowii* attracts tree shrews (*Tupaia montana*) that harvest nectar from the inside of the pitcher lid. The lid is bent backwards to allow the tree shrew to access the nectar while sitting on top of the large and sturdy pitcher. The wide-open funnel shape of the pitcher ensures that the shrew droppings end up in the trap. (d) *N. rajah* pitchers show similar adaptations and have been shown to be visited by tree shrews and nocturnal rats.
whether this could be a crucial factor for the attraction of vertebrates, we compared the nectar production of *N. rafflesiana* and *N. gracilis* to that of three sympatric species which were never observed to be visited by vertebrates foraging for nectar.

**Materials and methods**

*Field sites and study species*

Experiments and observations were conducted in three different sites of open, disturbed lowland heath forest (*kerangas*) in the Tutong and Belait districts of Brunei Darussalam, in August–September 2007, June–July 2011, February–April 2012, May 2013 and July–September 2014. Tutong site I contained six species of pitcher plants: *N. rafflesiana*, *N. gracilis*, *N. hemsleyana*, *N. ampullaria*, *N. bicalcarata* and *N. albo-marginata*. Of these, only *N. rafflesiana* and *N. gracilis* were found in Tutong site II. The Belait site, on the edge of Andulau forest reserve, contained *N. rafflesiana*, *N. gracilis*, *N. hemsleyana*, *N. ampullaria*, *N. bicalcarata* and *N. mirabilis* var. *echinostoma*. *N. rafflesiana* and *N. gracilis* were the most abundant species in the Tutong sites, while *N. ampullaria*, *N. bicalcarata* and *N. hemsleyana* were dominant in the Belait site. The two Tutong sites are characterised by open shrubland, and experience large fluctuations of temperature and relative humidity over the course of a day (Figure 2a, b). The Belait site consists of an open stream valley surrounded by a moderately disturbed mixed heath and freshwater swamp forest (Figure 2c).

*Observations*

Observations were made in Tutong sites I and II during all times of the day (and occasionally at night) and over multiple field seasons. Initial observations of sunbirds visiting pitchers were made by chance, whilst carrying out other experiments in the field. Follow-up observations focused specifically on the first 3 hours after sunrise, and the last hour before sunset, as these were found to be the times of peak vertebrate activity. Observations were made using Minox BL 8x32 BR binoculars, and photographs were taken with a Nikon D700 DSLR camera and a Nikon 80–400 mm/4.5–5.6G ED VR AF-S lens. Species were identified according to Myers (2009) and Payne et al. (1985).

*Nectar measurements*

We collected nectar from the peristomes of four species (*N. rafflesiana*, *N. hemsleyana*, *N. ampullaria* and *N. bicalcarata*) and the underside of the pitcher lid of *N. gracilis* in two field sites (Tutong I and Belait), and quantified the amount of sugar secreted per day. Measurements were conducted on aerial pitchers except in the case of *N. ampullaria* which only produces monomorphic, ground-type pitchers. For each species, eight pitchers (nine in the case of *N. gracilis*), each on a different plant, were randomly selected. Prior to the measurements, the peristomes (the lid in the case of *N. gracilis*)
Figure 2. (a) Typical habitat (Tutong site I) where we observed sunbirds and a tree shrew foraging on nectar of *Nepenthes rafflesiana* and *N. gracilis* pitchers. (b) Temperature and humidity measurements from the same site. The peak foraging times coincided with the times of high relative humidity from sunrise to about 10:30, and from about 17:00 until sunset. (c) The Belait site was less open, and surrounded by mature forest. We never observed vertebrates foraging on pitcher nectar in this site.
of all pitchers were repeatedly washed with distilled water to remove all nectar. Each pitcher was then enclosed in a fine-mesh gauze bag, and a sticky resin (The Tanglefoot Corp., Grand Rapids, MI, USA) was applied to the leaf base in order to prevent insects from accessing the pitcher. A stiff, transparent plastic sheet was fixed around the pitcher tendril to form an umbrella, shielding the pitcher against rain which could otherwise wash off the nectar (Figure 3).

Nectar was sampled every other day by gently wiping the peristome (lid) with a moist, c. 1 cm² piece of tissue paper (Kimwipe®, Kimberley-Clark, Reigate, UK) and then absorbing the moisture with small, triangular, highly absorbent surgical swabs (Sugi®, Kettenbach Medical, Eschenburg, Germany). Tissue paper and surgical swabs were held in self-closing surgical vessel clamps and collected in Eppendorff vials. The vials were stored, opened, over silica gel for several days until the samples were thoroughly dry.

Figure 3. Experimental setup to measure nectar production. Pitchers were enclosed in gauze bags to exclude visitors, and roofed with custom-made plastic umbrellas to prevent the nectar from being washed off by rain.
The nectar was then re-diluted in known quantities of distilled water (0.2–0.5 mL, depending on the amount of absorptive material), and the total amount of sugar was quantified using a temperature-compensated, handheld refractometer (ATAGO, L. Kübler, Karlsruhe, Germany).

**Results**

**Accounts of vertebrates visiting pitchers**

Four species of sunbirds and one species of tree shrew were observed harvesting nectar from aerial pitchers of *N. rafflesiana* and *N. gracilis*. We initially observed a male Van Hasselt’s sunbird (*Leptocoma brasiliana*) drinking nectar from the peristome of *N. rafflesiana* pitchers at dusk, in July 2011 (Tutong site I). Follow-up observations between 17:30 and 18:45 (sunset) over the following week yielded repeated visits of Van Hasselt’s and olive-backed sunbirds (*Cinnyris jugularis*) to *N. rafflesiana* pitchers. Sporadic observations in the same site (Tutong I) during the following two field seasons (spring 2012 and May 2013) showed that both species also visited *N. rafflesiana* pitchers in the morning, around 08:00, and occasionally as late as 10:30.

Regular observations from July to September 2014 in Tutong site II revealed two further species of sunbirds visiting pitchers: Brown-throated (*Anthreptes malacensis*) and crimson sunbird (*Aethopyga siparaja*). Van Hasselt’s and olive-backed sunbirds were also commonly observed collecting pitcher nectar in this site. Except for the crimson sunbird, all species were regularly observed drinking pitcher nectar in the morning, from shortly after sunrise (06:30) until about 10:30. Only the olive-backed sunbird was observed to be active during the hot daytime hours, and was never seen visiting pitchers at that time.

The crimson sunbird was only observed to visit pitchers once. Van Hasselt’s, Brown-throated and olive-backed sunbirds were regular visitors to pitchers of both *N. rafflesiana* and *N. gracilis* in Tutong site II. On any given morning, we would observe dozens of birds collecting nectar from both species. While the birds collected nectar exclusively from the peristome of *N. rafflesiana* (Figure 4a, b), they were only observed to harvest nectar from the underside of the pitcher lid of *N. gracilis* (Figure 4c, d).

On one occasion, we observed a lesser tree shrew (*Tupaia minor*) drinking nectar from the underside of *N. gracilis* pitcher lids in Tutong site II (Figure 5). This observation was made at 10:00 on 8 September 2014. The tree shrew was observed for about 5 minutes, climbing from pitcher to pitcher in a large *N. gracilis* plant and harvesting nectar.

**Nectar production**

The amount of secreted nectar varied considerably between the five investigated species. *Nepenthes rafflesiana* secreted the highest quantity of sugar, and *N. ampullaria* and *N. gracilis* the lowest (Figure 6). *Nepenthes gracilis* also secretes nectar onto the peristome (see Bauer et al. 2012 for a comparison of nectar secretion on the peristome and under the lid) but allocates a large proportion of its nectar secretion to the
underside of the pitcher lid. Particularly in the early morning, large droplets of accumulated nectar can be found under *N. gracilis* lids (*Figure 7*). We never observed vertebrates drinking nectar from the peristome of *N. gracilis*.

*Figure 4.* Sunbirds foraging on *Nepenthes* nectar in Tutong site II. (a) Female olive-backed sunbird (*Cinnyris jugularis*) and (b) male brown-throated sunbird (*Anthreptes malacensis*) drinking nectar from the peristomes of *N. rafflesiana* pitchers. (c, d) Male brown-throated sunbird (*A. malacensis*) harvesting nectar from the underside of the pitcher lid of *N. gracilis*.

*Figure 5.* (a, b) lesser tree shrew (*Tupaia minor*) collecting nectar from the lower lid surface of *Nepenthes gracilis* pitchers in Tutong site II.
Figure 6. Average nectar production per day for five *Nepenthes* species (*n* = 9 pitchers for *N. gracilis* and *n* = 8 for all other species). Values represent lid nectar for *N. gracilis* and peristome nectar for all other species. Bars denote medians, boxes represent the inner quartiles and whiskers include 1.5 times interquartile range. Circles represent outliers. Significant differences are marked with asterisks (Kruskal–Wallis test with post hoc Dunn comparisons; Bonferroni correction applied; ***: *P* < 0.001; *: *P* < 0.05).

Figure 7. Large nectar droplets (arrow) regularly accumulate on the lower lid surface of *Nepenthes gracilis* pitchers early in the morning.
Discussion

Our observations show for the first time that a diverse guild of nectar-harvesting vertebrates visits pitchers of two common lowland *Nepenthes* species, without providing any obvious benefit for the plants. The pitchers of the two species, *N. rafflesiana* and *N. gracilis*, are of a size and shape that make it virtually impossible for birds or tree shrews to leave their faeces inside the pitcher. The observed interaction is therefore almost certainly a case of nectar robbing with unidirectional benefit for the animal.

The peak times of nectar harvesting activity – from sunrise until approximately 10:30 and again in the late afternoon, from around 17:00 until sunset – coincided well with the times of day when the peristomes are wet (Bauer et al. 2008). The Tutong sites are both very open habitats, and in the absence of rain, the relative air humidity determines whether the pitcher peristomes are dry or wet. During the hottest (and driest, cf. Figure 2b) hours of the day, the water content of the peristome nectar evaporates, leaving a sticky, sugary residue that is hygroscopic and facilitates re-wetting when humidity levels rise again in the afternoon. Presumably, the liquid nectar, which is only present in the morning, evening and during the night, is easier to collect than the dry residue. In addition, birds and mammals might avoid being active in the open during the hottest hours of the day. Of the species we observed harvesting pitcher nectar, only the olive-backed sunbird was regularly seen foraging during the hot daytime hours; however, we never saw them visiting pitchers outside of morning or late afternoon times. This observation confirms that nectar-harvesting might only be profitable when there is enough air humidity to keep the nectar liquid.

The differences in nectar secretion measured for the five species of pitcher plant only partly explain why only two of them were observed to be visited by vertebrates. The large quantities of concentrated nectar secreted by *N. rafflesiana* should make this species particularly attractive as a food source; however, the amount of nectar secreted by *N. gracilis* was comparatively low. A combination of other factors is likely to play a role. First, *N. rafflesiana* and *N. gracilis* are far more abundant in the two Tutong sites than any of the other *Nepenthes* species: each site harbours several thousand individuals of both species in an area of approximately 1 km\(^2\) (Tutong I) and 0.5 km\(^2\) (Tutong II), respectively. In Tutong II, other *Nepenthes* species are absent altogether, while in Tutong I, they are present but at a low abundance. For instance, only three individuals of *N. albomarginata* were found, and *N. albomarginata* and *N. hemsleyana* were the only species found in the same open habitat as *N. rafflesiana* and *N. gracilis*. *N. ampullaria* and *N. bicalcarata*, the other two species occurring in Tutong I, were only found in closed forest patches at the southern edge of the site. Therefore, it is likely that the sunbirds (and the tree shrew) in these sites simply harvest nectar from the most abundant species. In addition, we spent more time around these species, making it more likely that we overlooked an occasional visit to one of the rarer species.

Focusing foraging activity on highly abundant species makes sense as it minimises the distances to travel between individual nectar sources. This distance is further reduced in *N. rafflesiana* and *N. gracilis* by the fact that mature individuals of both species can reach impressive size and bear hundreds of pitchers. The total amount of
secreted nectar per pitcher was found to be low in *N. gracilis*; however, during the early morning hours, the nectar under the lid of this species is typically concentrated in large droplets (Figure 7). This could make nectar foraging particularly economical. It would be interesting to investigate whether the chemical composition of the nectar varies between the different species. We only ever observed vertebrate visitors to aerial pitchers. It remains unclear whether this is due to a preference of the visitors for arboreal habitats, easier access to aerial pitchers because of the structural support offered by the surrounding vegetation, or differences between the quality and quantity of nectar secreted by aerial and ground pitchers.

We never observed birds or mammals harvesting nectar from pitchers in the Belait site. This site, c. 25 km to the southwest of the two Tutong sites, is surrounded by mature forest. The species composition and relative species abundance of the pitcher plant community as well as the bird community is markedly different from the Tutong sites. Sunbirds are less abundant in this site, and most pitcher plants grow on or just within the forest edge. The observed differences in visiting frequency might therefore be explained partly by species distribution, and partly by the preference of sunbirds for open habitats (Myers 2009; Carstensen et al. 2011).

While the sunbirds (and the tree shrew) gain energy from the sugary nectar they harvest, there is no conceivable benefit for the plant in this interaction. The size and position of the pitcher opening relative to the lid prohibit that vertebrate droppings could even accidentally fall into the pitcher, and observations of the typical positions of animals drinking nectar (Figures 4 and 5) confirm this. It is, however, possible that droppings fall on other parts of the plant or on the soil surrounding the plant’s roots, thereby increasing the general nutrient availability of the micro-habitat. In addition, nectar production is likely to come at a low cost in the open Tutong habitats where light and water availability is high.

The observed interactions between vertebrates and pitcher plants in Brunei might help to shed light on the evolution of intricate mutualistic relationships like those found in *N. lowii* and *N. rajah*. Our observations show that vertebrates are attracted by pitcher nectar and, in suitable habitat conditions, establish regular interactions with pitcher plants. This creates a situation where mutations leading to a pitcher geometry that enables the plants to ‘catch’ their visitors’ faeces could easily turn a unidirectional exploitation into a mutualistic relationship. The anecdotal reports of bird visitors to *N. lowii* and *N. faizaliana* pitchers (Clarke and Moran 1997; Phillipps et al. 2008) suggest that interactions between birds and pitchers might be widespread beyond the sites and species covered in the present study. As is the case with the *Nepenthes* species examined here, *N. faizaliana* is not known to have any mutualistic interactions with vertebrates (nor does it demonstrate any apparent adaptations for such interactions). Interestingly, the known vertebrate-mutualist *N. lowii* is also occasionally visited by nectar-feeding birds. This observation shows that *N. lowii* interacts with multiple vertebrate orders, but not necessarily always in a mutually beneficial way. Whether the birds have a mutualistic association with *N. lowii* remains to be seen. We hope that our observations inspire more research into the fascinating interaction between nectarivorous animals and pitcher plants. In particular, we would like to encourage the publication of further
records of such interactions as well as more quantitative accounts of the frequency and duration of vertebrate visits to pitchers.

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