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Harmless nectar source or deadly trap: *Nepenthes* pitchers are activated by rain, condensation and nectar

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The leaves of *Nepenthes* pitcher plants are specialized pitfall traps which capture and digest arthropod prey. In many species, insects become trapped by 'aquaplaning' on the wet pitcher rim (peristome). Here we investigate the ecological implications of this capture mechanism in *Nepenthes rafflesiana* var. *typica*. We combine meteorological data and continuous field measurements of peristome wetness using electrical conductance with experimental assessments of the pitchers' capture efficiency. Our results demonstrate that pitchers can be highly effective traps with capture rates as high as 80% but completely ineffective at other times. These dramatic changes are due to the wetting condition of the peristome. Variation of peristome wetness and capture efficiency was perfectly synchronous, and caused by rain, condensation and nectar secreted from peristome nectaries. The presence of nectar on the peristome increased surface wetness mainly indirectly by its hygroscopic properties. Experiments confirmed that pitchers with removed peristome nectaries remained generally drier and captured prey less efficiently than untreated controls. This role of nectar in prey capture represents a novel function of plant nectar. We propose that the intermittent and unpredictable activation of *Nepenthes* pitcher traps facilitates ant recruitment and constitutes a strategy to maximize prey capture.

Keywords: carnivorous plants; extrafloral nectar; leaf wetness; aquaplaning

1. INTRODUCTION

The interaction between predators and their prey has led to the evolution of adaptive strategies on both sides (Driver & Humphries 1988; Krebs & Davies 1997; Barbosa & Castellanos 2005). Most predators belong to the animal kingdom, but there are also several plant genera which have adopted carnivory as a means of acquiring nitrogen in nutrient-poor habitats. Carnivorous plants have evolved sophisticated adaptations to capture arthropod prey (Lloyd 1942; Juniper *et al.* 1989; Ellison & Gotelli 2001). In contrast to animal predators that spend only a fraction of their time hunting, traps of carnivorous plants are usually active all the time. The palaeotropic genus *Nepenthes* (Nepenthaceae) comprises more than 80 species of pitcher plants (Jebb & Cheek 1997). The leaves of these plants are mug-shaped organs specialized for attracting, capturing, retaining and digesting the prey. Arthropods attracted by extrafloral nectar and optical/olfactory cues (Moran 1996; Moran *et al.* 1999; Merbach *et al.* 2001) lose their foothold and fall into the digestive fluid which fills the lower part of the pitcher (Clarke & Wong 1997).

Several capture mechanisms have been proposed for *Nepenthes* pitchers. First, trapping is thought to be based on a slippery wax bloom on the inner pitcher wall of many *Nepenthes* species (Knoll 1914; Lloyd 1942; Juniper & Burras 1962; Juniper *et al.* 1989; Moran *et al.* 1999; Gaume *et al.* 2002). It is made up of microscopic, epicuticular wax crystal platelets which give rise to anti-adhesive surface roughness and easily break off, thus contaminating attachment structures and causing arthropods to slip (Knoll 1914; Juniper & Burras 1962; Gorb *et al.* 2005). Second, it has been suggested that anaesthesia by narcotic alkaloids causes prey capture in *Nepenthes madagascariensis* (Ratsirarson & Silander 1996). Only recently, we discovered that many *Nepenthes* species capture prey with the upper pitcher margin (the peristome, figure 1*a*,*b*; Bohn & Federle 2004). Its surface is characterized by a regular microstructure with radial ridges of smooth overlapping epidermal cells, which form a series of steps towards the pitcher inside (Owen & Lennon 1999). The peristome ridges mostly extend into tooth-like structures at the inner edge, in between which large extrafloral nectaries are situated. The microstructure, combined with hydrophilicity, renders the peristome completely wettable, in contrast to most other plant surfaces. Water droplets spread rapidly and form homogeneous thin films, which make the peristome extremely slippery for insects. When the peristome is wet, the fluid films prevent the insects' tarsal adhesive pads from making close contact with the surface, similar to the aquaplaning of a car tyre on a wet road. In addition, the anisotropic microstructure of the peristome surface allows interlocking of claws only while the insect is running towards the pitcher inside, but not on the way out (Bohn & Federle 2004).

This wetness-based capture mechanism of *Nepenthes* pitcher plants has interesting ecological implications. As dry peristomes are not slippery for insects (Bohn & Federle 2004), pitchers only work as effective insect traps

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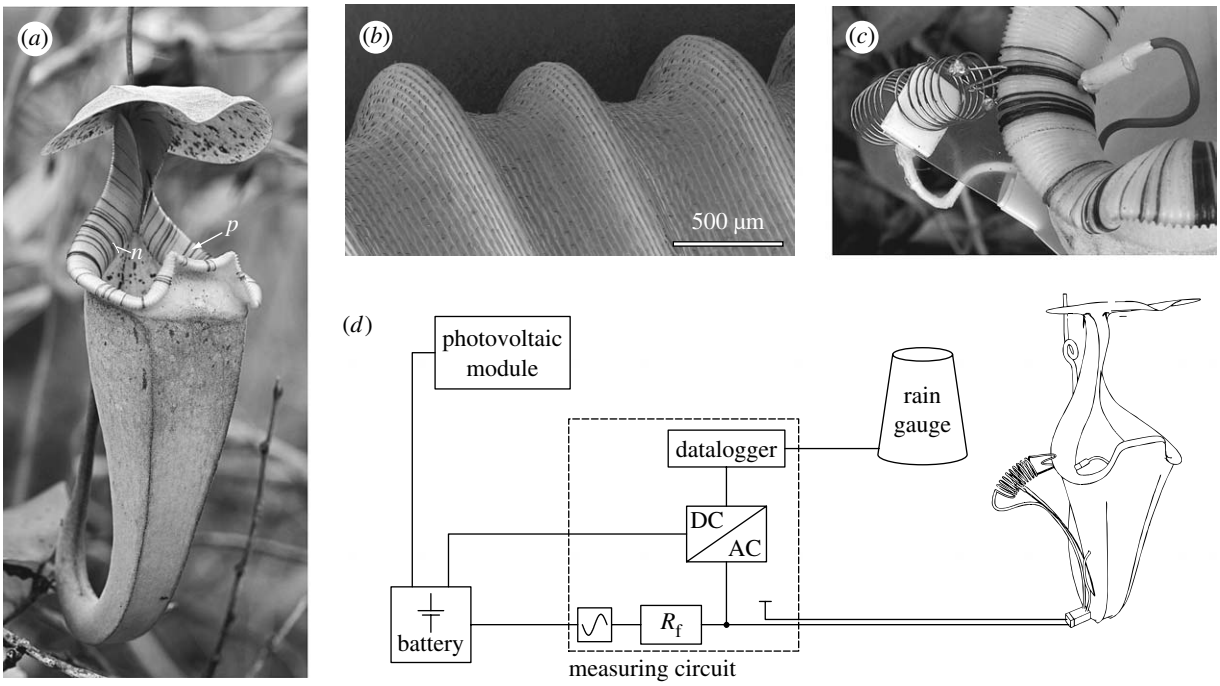

Figure 1. (*a*) Upper pitcher of *Nepenthes rafflesiana* var. *typica* (p, peristome; n, position of peristome nectaries). (*b*) SEM image showing the regular microstructure of the peristome. Scale bar, 500 µm. (*c*) Peristome of upper pitcher of *N. rafflesiana* var. *typica* with magnetic electrode (inside) and spring electrode (outside). (*d*) Schematic of experimental setup used to measure the wetness of the peristome. The electrical resistance between both electrodes provides a measure of the degree of peristome wetting.

when their peristomes are wet. However, it is still unclear when and how this is achieved under natural conditions. Water films on the peristome may originate from rain, condensation and nectar secretion, of which only the last mechanism provides the possibility of an active regulation by the plant. The interaction of all three factors could lead to a complex pattern of trap activation. Here we study the temporal variation of peristome wetting and capture efficiency in the field. We investigate (i) when and by which mechanism peristomes are wetted under natural conditions and (ii) whether pitcher trapping efficiency changes with daytime and weather conditions as predicted from the condition of the peristome.

2. MATERIAL AND METHODS

Experiments were performed on *Nepenthes rafflesiana* var. *typica* at a site with heavily degraded kerangas forest on white sandy soil in Brunei, northern Borneo (4°34′ N, 114°25′ E). The vegetation is open, and temperatures ranged from 24°C in late night to 38°C in early afternoon. *N. rafflesiana* var. *typica* is abundant and occurs sympatrically with *Nepenthes gracilis*.

(a) *Measurement of peristome wetness using electrical conductance*

We developed a method to continuously monitor the wetness of pitcher peristomes in the field. It was determined from the resistance between two electrodes attached to the inner and outer margins of the peristome. The inner contact was held in position by a tiny magnet. Its lead was passed to the outside through a small hole in the pitcher wall. The outer contact was a small spring with a V-shaped tip. It was mounted on a plastic holder which was attached to the pitcher using adhesive tape (figure 1*c*,*d*).

An electrical circuit containing a potential divider with a fixed resistor of 1 MΩ was used to record the electrical resistance of the peristome as a voltage (figure 1*d* and electronic supplementary material, figure S3). The circuit used AC with $U = 12 V_{pp}$ and a frequency of 1 kHz. Data were recorded from several pitchers simultaneously with a sampling frequency of $1\ \mathrm{min}^{-1}$ using a µLog VL 100S eight-channel data logger (a.b.i. data, Brussels). Voltage values were converted to conductance according to the following equation:

$$\frac{1}{R_p} = \frac{U - U_{measured}}{R_f U_{measured}}, \tag{2.1}$$

where R_p is the peristome resistance; R_f is the fixed resistor; and $U_{measured}$ is the measured voltage. The electrical conductance reflects the degree of surface wetting. We compared the mean conductance of three pitchers for a period of 24 hours with that of visual assessments of peristome wetness on 30 pitchers (16 checks in intervals of 90 min). We classified the observed states of peristome wetness in four categories ranging from completely dry to wet (continuous fluid film on the surface). The results of conductance measurements and personal observations were strongly correlated (Spearman's rank test: $n = 16$, d.f. $= 14$, $\rho = 0.80$, $p < 0.01$). Owing to variable electrolyte content of the fluid on the peristome surface and the non-standardized distance and contact area of the electrodes, our method does not allow conclusions about the absolute amount of fluid present (cf. Klemm *et al.* 2002). However, since the position of electrodes remained constant during the experiments, temporal variations of peristome wetness could be reliably recorded.

In addition to the measurements of peristome wetness, we continuously recorded air temperature and relative humidity using Tinytag Plus data loggers (Gemini Data Loggers, Chichester), and monitored precipitation with a tipping bucket rain gauge (Rain Collector II, Davis Instruments

Corp., Hayward) connected to one channel of the μLog VL 100S data logger.

(b) *Measurement of capture efficiency*

To bring large numbers of ants into contact with *N. rafflesiana* pitchers, we collected partial colonies (50–300 workers) of a *Camponotus* species belonging to the *C.* (*Colobopsis*) *saundersi* group (body length approx. 10 mm) on the day before the experiments. We kept them (fed with honey–water) in plastic containers side-coated with slippery Fluon (Whitford, Diez) to prevent ants from escaping. To start the experiment, live *N. rafflesiana* pitchers were placed upright on a support inside the plastic container so that the ants had access. The ants ran onto the pitchers to explore the new object, that is, they were not foraging for food. We investigated whether experimental wetting of the peristome in *N. rafflesiana* var. *typica* pitchers increased the capture efficiency, as we demonstrated previously for *Nepenthes bicalcarata* (Bohn & Federle 2004). We tested the effects of wetting (using an atomizer), drying (with dust-free tissue) and re-wetting (see figure S1 and video in the electronic supplementary material).

To investigate the correlation of peristome surface conductance and trapping efficiency, we performed consecutive running experiments and simultaneous voltage measurements on the same pitchers in the field. The digestive fluid was removed for the duration of the experiment to reduce the consumption of test animals. The ants were recorded while running on the pitcher using a Sony DCR-PC120E video camera. Videotapes were analysed by counting the number of capture events in relation to the number of peristome visits. A visit was defined as an ant stepping onto the peristome with more than three legs, no matter if the peristome was entered from the inside or the outside. Re-entering of the peristome was counted as a new visit. This definition ensured that all ants were counted that could potentially be trapped. Other, more rigorous definitions (e.g. all legs in contact with the peristome) would have led to even more clear-cut effects.

(c) *Experiments on pitchers with removed peristome nectaries*

To evaluate the contribution of nectar secretion to peristome wetting, we abscised the peristome nectaries of two pitchers. This was achieved by cutting an approximately 3 mm wide strip off the inner margin of the peristome using a fine scalpel. Even though this treatment lowered the capture rate, pitchers devoid of peristome nectaries were still highly effective insect traps when wet (see figure S2 in the electronic supplementary material). We monitored peristome conductance of these pitchers simultaneously with that of two unmanipulated control pitchers on the same plants. This experiment was repeated on another set of 2×2 pitchers one month later. To differentiate between the direct and indirect effects of nectar on peristome wetness, we calculated for each pitcher 'relative conductances' ranging from 0 to 100% and determined the time when the peristomes reached 50% re-wetting in the afternoon (only days without precipitation analysed). If pitchers directly wet their peristomes with fluid nectar, pitchers with abscised nectaries should reach 50% re-wetting later than intact pitchers. However, if peristome nectar films mainly originate by rehydration of dried nectar, pitchers with and without nectaries should reach 50% re-wetting at the same time which would largely depend on air humidity.

To investigate the relevance of nectar for prey capture, we performed a series of simultaneous running experiments on three differently treated pitchers growing on the same plant. On one pitcher, we abscised the nectaries and rinsed the peristome with distilled water to remove all nectar. The peristome of the second pitcher was only rinsed, and the third pitcher remained untreated.

3. RESULTS

(a) *Temporal variation of capture efficiency*

The capture efficiency of *N. rafflesiana* var. *typica* pitchers showed a pronounced diurnal variation (figure 2). Pitchers did not capture any ant during most of the day but they were highly efficient traps in the evening, night and early morning (capture efficiency ranging from 0% to more than 80%). The most significant changes in capture rates took place from 07.00 to 08.00 and from 17.30 to 18.00 (conventional and Craddock–Flood's chi-squared tests, $p < 0.001$, for sample sizes see figure 2).

(b) *Capture efficiency and peristome wetness*

Experimental wetting of the peristome of *N. rafflesiana* var. *typica* pitchers increased the capture efficiency from 0% to more than 60%, similar to our earlier findings for *N. bicalcarata* (Bohn & Federle 2004, see figure S1 in the electronic supplementary material). Under natural conditions, daily fluctuations of peristome wetness also give rise to dramatic changes in capture efficiency, as revealed by our combined measurements of peristome surface conductance and capture rate.

Changes in capture efficiency and peristome wetness were almost perfectly synchronized (figure 2), the correlation between both being positive and highly significant (Spearman's rank test: $n = 14$, d.f. $= 12$, $\rho = 0.87$, $p < 0.01$). When the peristome was dry (low conductance), its surface was not at all slippery for ants. Under wet conditions, however, most ants slipped and fell into the pitcher as soon as they stepped onto the peristome.

(c) *Effects of rain and condensation*

Peristome wetness showed regular diurnal oscillations with higher conductance during the night (figure 3). Superimposed on this pattern were peaks caused by precipitation which generally led to a strong and rapid increase in surface conductance. Parallel measurements from the same pitcher and from adjacent, simultaneously monitored pitchers showed very similar curve progressions even though their absolute conductance differed depending on the conditions of the electrode contact.

At times without precipitation, the conductance curve largely followed the relative air humidity curve. Dew formation at night was observed regularly. During the second half of the night, peristomes were generally wet, and hydrophobic leaf surfaces were densely covered with dewdrops. The capacity of dew to wet the peristome sufficiently for prey capture was proven in running experiments with ants on pitchers without nectaries during a rainless night (figure 5*c*). In this experiment, all other possible sources of wetting but dew had been excluded.

(d) *Effect of peristome nectar*

In the evening hours, we regularly observed large amounts of liquid nectar on the peristomes of *N. rafflesiana* var. *typica*, suggesting that nectar secretion plays an important role in the wetting of the peristome. We tested the

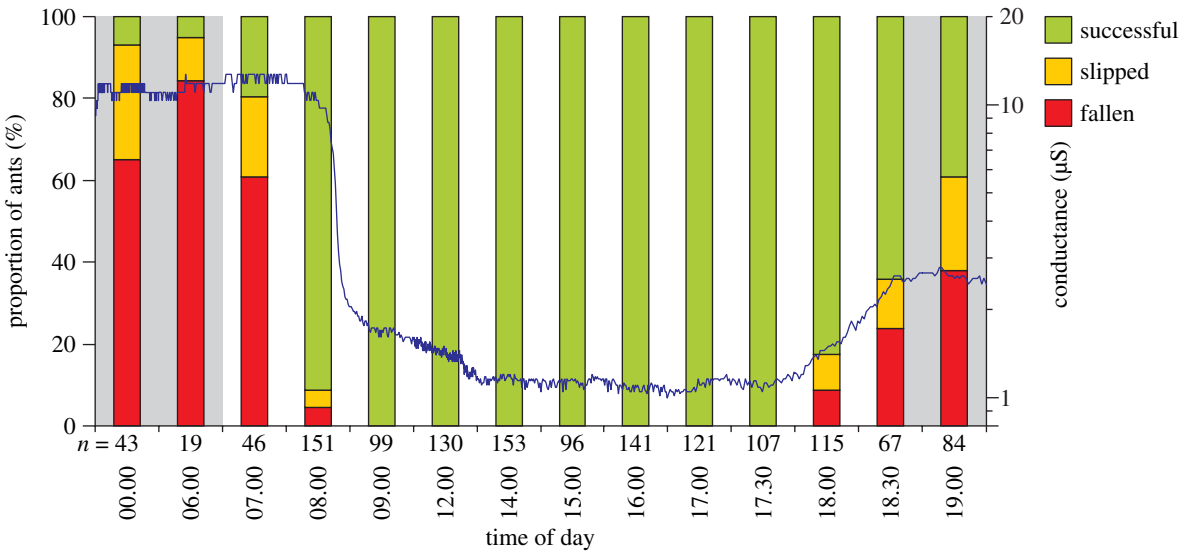

Figure 2. Temporal variation of peristome surface conductance and capture rate as obtained in a time series of running experiments with *Camponotus* (*Colobopsis*) sp. ants on a *N. rafflesiana* var. *typica* pitcher. Note that the time scale is not evenly divided.

contribution of nectar by evaluating the effect of nectary abscission on peristome wetness and prey capture. Visual assessments and conductance measurements confirmed that the peristomes without nectaries were distinctly drier than the control group at most times of the day. Moreover, the conductance measurements revealed an interesting phenomenon (figure 4*a*). In the first days after nectary abscission, conductance curves of manipulated and unmanipulated peristomes progressed similarly on a comparable level (Mann–Whitney *U*-test of 24th h means, $n=8$, $U=21.0$, $p \gg 0.05$). However, after the first heavy downpour had rinsed off the nectar, the conductance curves of manipulated pitchers still showed the same temporal variation but were shifted to a markedly lower level while those of unmanipulated pitchers remained unaffected (figure 4*a*). After the rain, the difference between conductance values of peristomes with and without nectaries was highly significant (Mann–Whitney *U*-test of 24 h means, $n=42$, $U=377.0$, $p<0.001$). This indicates that the presence of concentrated nectar on the peristome surface considerably enhances peristome wetting. The largely unchanged time course of peristome conductance in pitchers without nectaries shows that the observed patterns are not caused by plant-induced variations of nectar electrolyte concentration.

Rain increased the conductance of all peristomes to a comparable level (figure 4*b*). Thus, the absence of nectar had no effect on the wetting by rain, but it decreased water condensation from the air. Surprisingly, our data provide no evidence of direct wetting of the peristome surface by secretion of liquid nectar. In both experiments, the daytime of 50% re-wetting did not differ significantly between pitchers with and without peristome nectaries (Kruskal–Wallis tests: $n_1=15$, $H_1=6.47$, $p_1 \gg 0.05$; $n_2=9$, $H_2=2.37$, $p_2 \gg 0.05$; figure 4*c*). This suggests that nectar is mainly secreted at times of high humidity when the peristome is already fully wetted, that is, between the evening and early morning. We conclude that even though nectar plays an important role for peristome wetting, its contribution is mainly indirect as an enhancer of water condensation.

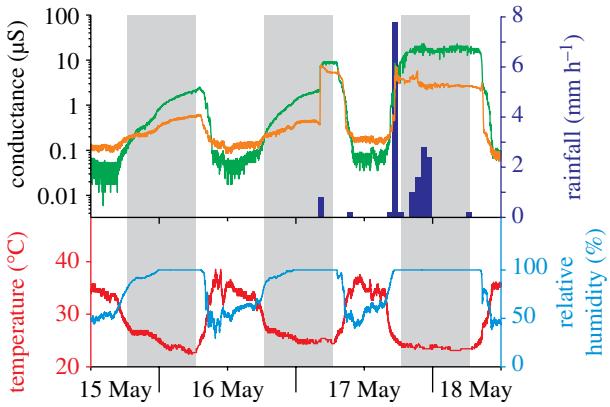

Figure 3. Diurnal variation of peristome surface conductance of two *N. rafflesiana* var. *typica* pitchers (top, green and orange curves), precipitation (top, blue bars) and meteorological data (bottom, red and blue curves) at the study site in Brunei. Nights are marked by grey background. High conductance indicates a wet peristome.

The running experiments with ants on pitchers with different manipulations clearly showed the importance of nectar for prey capture (figure 5). Removal of the nectaries had no visible effect on the ants' behaviour and many workers were running on the peristome. While both the unmanipulated and the intact but rinsed pitcher exhibited the usual increase in slipperiness and trapping efficiency (pitchers not significantly different at any time; Fisher's exact tests for 'fallen' versus 'not fallen': $p>0.05$), the pitcher without peristome nectaries remained completely ineffective throughout the afternoon (highly significant differences to pitchers with nectaries at 18.25–18.55 and 19.15–20.00; Bonferroni-corrected Fisher's exact tests: $p<0.001$). Only in the middle of the night did the pitcher without nectaries also become slippery so that the capture efficiency of all pitchers was again similar (Fisher's exact test: $p>0.05$). As wetted pitchers with abscised nectaries are still effective traps (see figure 5*c* and electronic supplementary material, figure S2), this effect cannot be explained by the mechanical effects of the manipulation

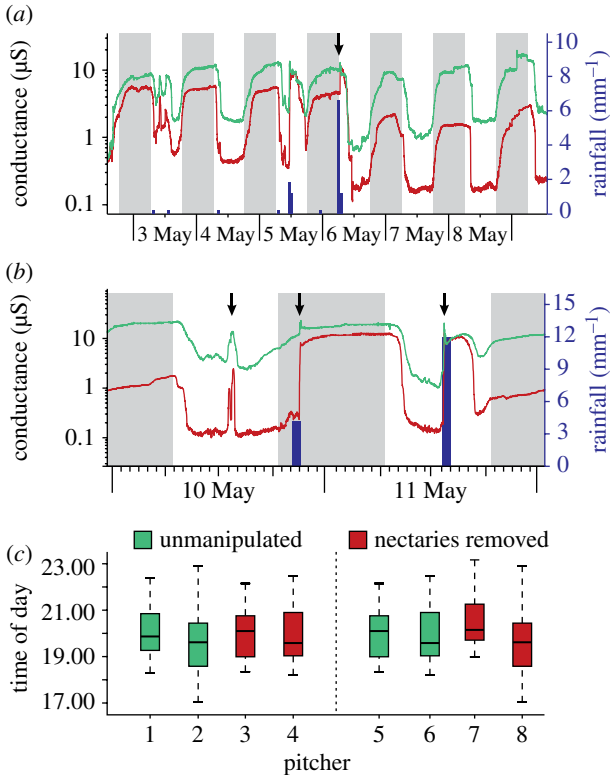

Figure 4. (*a*) Comparison of peristome surface conductance of *N. rafflesiana* var. *typica* pitchers with (green curve) and without (red curve) peristome nectaries (means plotted). Nights are marked by grey background. Nectaries were abscised on 2 May. Both curves diverge markedly after the first heavy rain (arrow). (*b*) Later stage of the same experiment. Rainfall (black arrows) increases the conductance of both groups of peristomes to about the same level (light daytime rainfall on 10 May not recognized by the rain gauge). (*c*) Daytimes of 50% peristome re-wetting in pitchers with (green boxes) and without (red boxes) peristome nectaries. Pitchers 1–4 were monitored from 27 March to 2 May 2006 and pitchers 5–8 from 2 May to 20 May 2006.

but it demonstrates that the peristome nectaries facilitate prey capture via enhanced water condensation.

4. DISCUSSION

(a) *Activation of traps by peristome wetting*

Our results show that the capture efficiency of *N. rafflesiana* var. *typica* pitchers changes dramatically over time. The close correlation of trapping efficiency and peristome wetness (figure 2) demonstrates that the temporal variation can be completely attributed to changes in the degree of peristome wetting. These findings confirm the importance of the peristome and of 'insect aquaplaning' for prey capture by *Nepenthes* species (Bohn & Federle 2004) under field conditions. Although the running experiments with ants did not represent natural capture events, they accurately indicate the effectiveness of the pitcher traps. The extreme temporal variation of pitcher capture efficiency has not been documented previously. It explains why the trapping function of the peristome has long remained overlooked (Lloyd 1942; Juniper *et al.* 1989; Gaume *et al.* 2002).

Why should a carnivorous plant have evolved a trapping mechanism which is often ineffective and thus seemingly ill designed? It has been suggested that accumulation of excessive amounts of prey could cause putrefaction and thus an earlier death of the pitcher (Clarke & Kitching 1995). On the other hand, prey digestion is known to be accomplished to a large degree by the pitcher infauna under natural conditions (Bradshaw & Creelman 1984) and pitchers can capture vast amounts of prey without being harmed (Merbach *et al.* 2007). Therefore, it seems unlikely that there is a selective pressure for prey reduction in *Nepenthes*. On the contrary, we propose that the temporary ineffectiveness of the trap is actually a strategy for maximizing prey capture. Surprise and unpredictability are essential elements of animal hunting behaviour (e.g. Driver & Humphries 1988). Animal predators show behavioural adaptations that make them difficult to detect and unpredictable, such as irregular hunting, aggressive mimicry (e.g. Stowe *et al.* 1987), stalking behaviour and ambushing. Besides the direct advantage gained by a surprise attack, the unpredictability of predator behaviour will make the evolution of specific avoidance behaviours more difficult, and thus ensure sustained prey capture success in the long term.

The trapping in *N. rafflesiana* var. *typica* pitchers bears interesting parallels to the strategies of animal predators. Although the general pattern of diurnal variation of peristome wetness was largely consistent over time, the exact state of wetting at a given time varied from day to day and between pitchers, due to changes in weather conditions and spatial variations in microclimate. Many *Nepenthes* species (e.g. *N. bicalcarata*) thrive in less open and more humid habitats than our study site. In these habitats, the diurnal variation of humidity is less regular and less predictable. As a consequence, pitcher-visiting insect species cannot easily counteradapt and avoid being trapped simply by restricting foraging to a particular time of day. Similarly, on an individual scale, insects can hardly learn to avoid pitcher plants because they mostly die from their first negative experience.

Nepenthes pitcher plants might also benefit more directly from the temporary ineffectiveness of the trap. A major proportion of prey in most *Nepenthes* species consists of ants (Jebb 1991; Moran 1996), which can efficiently exploit patchy food resources by recruiting nestmates (Hölldobler & Wilson 1990). Tan (1997) proposed that low pitcher capture rates in general should result in a greater number of surviving 'scout' ants, which then recruit more nestmates to the pitchers. Therefore, low capture efficiency might ultimately result in increased prey numbers. However, our findings suggest that the variable capture efficiency results in a temporal separation of ant (scout) attraction by nectar and the capture of recruited nestmates. Such a strategy might yield more prey than a continuously low capture efficiency.

(b) *Natural sources of peristome wetting*

The conductance measurements revealed that all three possible mechanisms of peristome wetting—rain, dew and nectar secretion—operate in *N. rafflesiana* var. *typica*. The impact of rain was particularly obvious in recordings of daytime rainfalls (figure 4*b*). Even though the pitcher lid shields the pitcher sufficiently against flooding, it does not prevent the peristome from being wetted by rain. A possible consequence of the pitcher activation by rainfall is that pitchers capture more prey during rainy seasons,

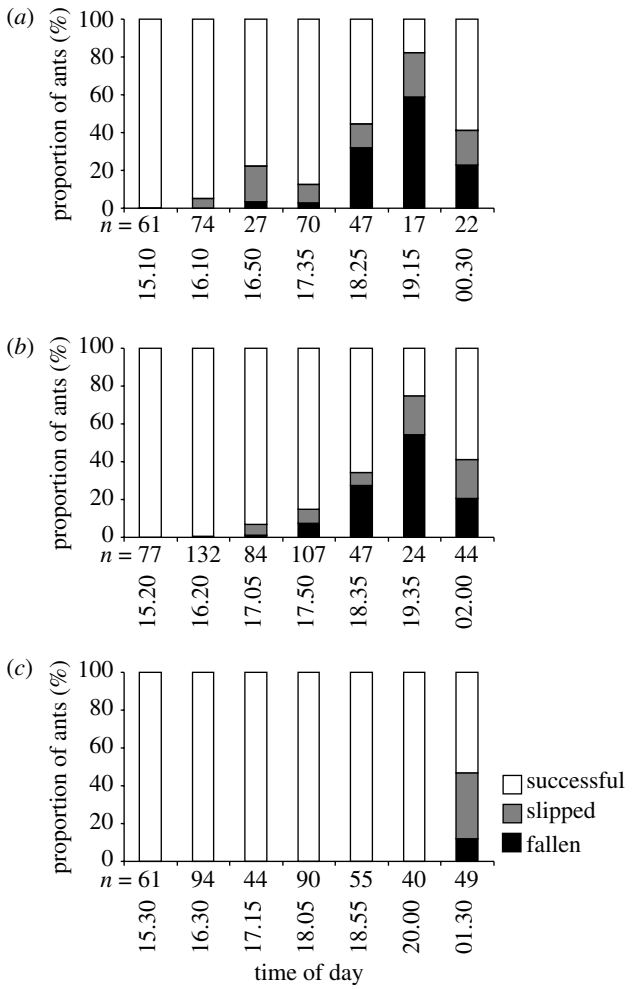

Figure 5. Capture efficiency and peristome wetting measured simultaneously on three *N. rafflesiana* var. *typica* pitchers from the same plant: (*a*) unmanipulated control, (*b*) intact nectaries, peristome rinsed with water and (*c*) nectaries removed and peristome rinsed with water. All manipulations were carried out 3 days before the start of the observations.

which may also be periods of faster growth and greater demand of nutrients.

At times without precipitation, peristome conductance largely followed the diurnal changes of air humidity. The open vegetation at our study site and the resulting wide range of temperatures measured in the diurnal cycle (figure 2) entailed pronounced oscillations of relative air humidity and thus enhanced the diurnal variation of peristome wetness and capture efficiency. Measurements and observations on pitchers without nectaries clearly confirmed that high air humidity at night is sufficient to wet the peristomes.

The comparison of pitchers with and without nectaries demonstrated the importance of nectar for peristome wetting. We were able to show that the main contribution of nectar towards peristome wetting is indirect by facilitating water condensation, while an influence of direct wetting could not be shown. Sugar and nectar are well known for their hygroscopic properties (Browne 1922), and spot checks of freshly secreted peristome nectar in *N. rafflesiana* var. *typica* indicated high sugar concentrations of 10–40% (W. Federle 2005, unpublished results). Owing to its spreading on the completely wettable peristome surface, the nectar is exposed to wind and sunshine which facilitate evaporation. This is in striking contrast to the extrafloral nectaries of many other plants which are often cup-shaped and designed to minimize evaporation in order to keep the nectar attractive and consumable to insects (Elias 1983). Evaporation can lead to nectar crystallizing at daytime and becoming liquid again by water absorption at night (Deppe *et al.* 2000). During hot and dry days, we regularly observed dried nectar on the peristome surface of *N. rafflesiana* var. *typica*. Considering the role of dried nectar in the re-wetting of the peristome, nectar evaporation (mediated by the structure of the peristome) may be less adversarial for *Nepenthes* than it is for other plants. Despite the indirect contribution of nectar to peristome wetting, it is possible that pitcher plants actively regulate the degree of wetting by adjusting the amount of nectar secretion.

The role of nectar in prey capture in *Nepenthes* is remarkable because it involves a novel, purely mechanical function of nectar. Usually, nectar is used by plants to attract and/or reward insects in the context of pollination and biotic defence (Herrera & Pellmyr 2002; Wäckers *et al.* 2005). The nectar in *N. rafflesiana* var. *typica* also serves the attraction of prey insects. However, its function to increase the mechanical efficiency of the pitcher trap represents the acquisition of a new role. Further studies should establish whether the peristome nectar in *Nepenthes*, owing to its exceptional function, differs in its chemical composition from pure 'attraction' nectars. If the peristome nectar was mainly optimized for facilitating water condensation, one might expect a smaller concentration of (expensive) amino acids and a larger proportion of (cheap) sugars.

Peristome nectar appears to play a less important role in many other *Nepenthes* species. For example, we found that the other variety of *N. rafflesiana* co-occurring in Brunei, var. *elongata*, produces far less peristome nectar (U. Bauer 2007, unpublished results). However, it possesses slippery wax crystals on its inner pitcher walls and therefore does not rely exclusively on 'peristome aquaplaning' for prey capture. In contrast to the 'aquaplaning' mechanism, the efficiency of slippery wax crystals is probably independent of weather conditions and not temporally variable. Further comparative work is needed to determine whether the possession of an additional, wetness-independent capture mechanism enables waxy *Nepenthes* species to colonize a broader range of habitats than their congeners.

Specialized pitcher peristomes with strikingly similar surface structures are found in several non-related genera such as *Nepenthes* (Nepenthaceae), *Cephalotus* (Cephalotaceae) and *Darlingtonia* (Sarraceniaceae). Moreover, all these plants possess nectaries located on the peristome (Juniper *et al.* 1989). We conjecture that all these plants not only possess a similar wetness-based capture mechanism but also exhibit a temporally variable trapping efficiency as reported in this study.

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