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How a pitcher plant facilitates roosting of mutualistic woolly bats

Yen Shan Lim[1], Caroline R. Schöner[2], Michael G. Schöner[2], Gerald Kerth[2], Daniel G. Thornham[3,4], Mathias Scharmann[3,5] and T. Ulmar Grafe[1]

[1]*Faculty of Science and Institute for Biodiversity and Environmental Research, Universiti Brunei Darussalam, Brunei Darussalam,* [2]*Zoological Institute and Museum, Greifswald University, Greifswald, Germany,* [3]*Insect Biomechanics, Zoology Department, University of Cambridge, Cambridge, UK,* [4]*Biology Division, University of South Wales, Pontypridd, UK and* [5]*Institute of Integrative Biology, ETH Zurich, Zurich, Switzerland*

ABSTRACT

Question: How does the pitcher plant *Nepenthes hemsleyana* facilitate roosting of mutualistic bats?

Hypothesis: Pitchers have adaptations that match the shape and body size of small woolly bats.

Organisms: The pitcher plant *Nepenthes hemsleyana*, its close relative *N. rafflesiana*, and the woolly bat *Kerivoula hardwickii.*

Field sites: Peat swamps and heath forests in western Brunei Darussalam on the island of Borneo.

Methods: We measured various morphological traits of *N. hemsleyana* that might facilitate bat roosting. We compared these traits with those of *N. rafflesiana*, which is not visited by bats. We compared the sizes and characteristics of the pitchers with the body sizes of roosting bats.

Conclusions: As predicted, aerial pitchers matched the body size of bats and had lower digestive fluid levels than pitchers of a close relative. Thus, small morphological differences between closely related species have caused rapid dietary niche divergence.

Keywords: Borneo, carnivorous plants, *Kerivoula hardwickii*, mutualism, *Nepenthes*, roosting behaviour.

INTRODUCTION

Carnivorous plants trap arthropod prey using a variety of independently evolved trapping mechanisms (Darwin, 1875; Juniper *et al.*, 1989; Ellison *et al.*, 2003; Phillipps *et al.*, 2008; Bauer *et al.*, 2011). The pitcher plants of the genus *Nepenthes* (Nepenthaceae) capture and digest arthropod prey in their fluid-filled pitchers. Pitcher shapes and sizes, growth forms, and habitat preferences are

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Correspondence: T.U. Grafe, Faculty of Science and Institute for Biodiversity and Environmental Research, Universiti Brunei Darussalam, Tungku Link, Gadong 1410, Brunei Darussalam. e-mail: grafe@biozentrum.uni-wuerzburg.de

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highly variable within this genus. Over 120 species occur across their palaeotropical range, with the centre of diversity in Borneo (Meimberg and Heubl, 2006; McPherson *et al.*, 2009).

Pitcher-associated phenotypes are highly polymorphic even at the species level. As such, they are assumed to be under diversifying selection and play a crucial role in the genesis of plant diversity (Clarke, 1997; Phillipps *et al.*, 2008). Studies of the ecology of *Nepenthes* have typically focused on pitcher-related characteristics, particularly the structures and mechanisms related to attracting and trapping prey (e.g. Bohn and Federle, 2004; Bauer and Federle, 2009; Gaume and Di Giusto, 2009). These include the nectar glands (Merbach *et al.*, 2001; Bauer *et al.*, 2008), olfactory and visual cues (Moran, 1996; Moran *et al.*, 1999, 2012; Bauer *et al.*, 2011), the slippery peristome surfaces (Bauer *et al.*, 2009, 2015), viscoelastic digestive fluids (Gaume and Forterre, 2007), and waxy inner surfaces (Gaume *et al.*, 2004).

These studies have also revealed that there is more to *Nepenthes*' plant–animal interactions than carnivory. For example, *N. bicalcarata* Hook. f. has developed a mutualistic relationship with the swimming ant *Camponotus schmitzi* Stärke, which enhances trapping efficiency by regularly cleaning the pitcher rim (peristome) (Thornham *et al.*, 2012) and prevents infaunal larvae from leaving the pitchers as adults (Scharmann *et al.*, 2013) in exchange for extra-floral nectar and refuge in the pitcher's tendril (Clarke and Kitching, 1995; Bonhomme *et al.*, 2011a; Bazile *et al.*, 2012). Furthermore, associations between *Nepenthes* and small mammals have been documented. Tree shrews [*Tupaia montana* Thomas (Clarke *et al.*, 2009; Chin *et al.*, 2010; Greenwood *et al.*, 2011)] and nocturnal rats [*Rattus baluensis* Thomas (Wells *et al.*, 2011)] feed on pitcher lid exudates of montane *Nepenthes* species [*N. rajah* Hook. f., *N. lowii* Hook. f., and *N. macrophylla* (Marabini) Jebb and Cheek], whose large pitchers are modified to 'capture' the feces of these small mammals. The focus of this study is another mammal–pitcher plant relationship: *N. hemsleyana* Macfarlane obtains nitrogen from the feces of *Kerivoula hardwickii* Horsfield (Hardwicke's woolly bat) that roosts in its aerial pitchers (Grafe *et al.*, 2011).

Study species

Nepenthes hemsleyana was previously reported as the elongate form of *N. rafflesiana* Jack [*elongata nom. nud.* (Cheek and Jebb, 2001; Phillipps *et al.*, 2008)]. In northwest Borneo, the 'elongate' and 'typical' varieties can often be found in close sympatry. The elongate variety was recently elevated to species status by Clarke *et al.* (2011), who gave it the name *N. baramensis*. However, this name is a junior synonym of *N. hemsleyana* Macfarlane (Macfarlane, 1908; Scharmann and Grafe, 2013).

Nepenthes hemsleyana appears to have a relatively narrow distribution in northwestern Borneo, with high densities found in the interior peat swamps and heath forests of Brunei Darussalam (Clarke *et al.*, 2011). In contrast, its close relative *N. rafflesiana* Jack has a broad biogeographical distribution and is relatively common in heath forests with acidic soils. Like most *Nepenthes* species, *N. hemsleyana* and *N. rafflesiana* plants produce lower and upper pitchers over their lifetime (Cheek and Jebb, 2001). The upper or 'aerial' pitchers are conical in shape. In *N. hemsleyana*, the aerial pitchers are divided into an upper waxy zone and a lower secretory zone, whereas *N. rafflesiana* aerial pitchers only have a secretory zone (Gaume and Di Giusto, 2009; Bauer *et al.*, 2011).

Nepenthes rafflesiana catches more prey of higher diversity (Moran, 1996; Bauer *et al.*, 2008, 2009, 2011) and has a higher pitcher fluid viscosity and more human-perceptible fragrances than *N. hemsleyana* (Moran, 1996; Clarke *et al.*, 2011). *Nepenthes hemsleyana* produces longer and more tapered pitchers that are much less effective as an insect trap. The aerial pitchers of *N. hemsleyana* obtain an average of 33.8% (and up to 56%) of the plant's foliar nitrogen from bat feces and urine, whereas bats avoid the fluid-filled ground pitchers, which have a distinctly different morphology (Grafe *et al.*, 2011). Thus, different pitcher structures seem to facilitate alternative prey-trapping strategies in these *Nepenthes* species (Gaume and Di Giusto, 2009; Bauer *et al.*, 2011). Preliminary genetic data indicate that *N. hemsleyana* and *N. rafflesiana* are direct sister taxa (M. Scharmann, unpublished). Due to their close relatedness, *N. hemsleyana* and *N. rafflesiana* can be used as model taxa to investigate the evolution of different nutrient acquisition strategies.

The woolly bat *K. hardwickii* (Vespertilionidae) is a small gleaning bat that lives and forages in forest interiors in large parts of tropical Asia (Payne *et al.*, 1985). Multiple lines of evidence strongly suggest that numerous genetic lineages, if not species, exist under this name (Douangboubpha *et al.*, 2015). In Brunei, *K. hardwickii* is abundant in forests that contain pitcher plants (Struebig *et al.*, 2012; Schöner *et al.*, 2013), suggesting a link in the geographic distribution of this subspecies (or cryptic species) and *N. hemsleyana*, although the bats do occasionally use alternative roosts [e.g. *N. bicalcarata* (Schöner *et al.*, 2013)]. Previous studies that measured pitcher length and diameter have highlighted obvious allometric differences between *N. hemsleyana* and *N. rafflesiana* (Moran, 1996; Gaume and Di Giusto, 2009; Grafe *et al.*, 2011). However, these measures provide only a partial answer to the suitability of pitchers as roosting sites for woolly bats because there are no data on bat body size and how well they fit into the pitchers that they choose.

This study aims to compare key morphological traits of *N. hemsleyana* and *N. rafflesiana* relevant to the roosting behaviour of *K. hardwickii*. We hypothesized that the aerial pitchers of *N. hemsleyana* are matched in size and shape to the body size of woolly bats and that they have lower digestive fluid levels and thus offer more space for roosting bats than the sympatric, closely related *N. rafflesiana*. In particular, we hypothesized that pitcher orifice diameter, the degree of pitcher tapering, fluid level, and space availability between the two species of pitcher plants would differ significantly. If so, relatively minor morphological modifications of trap characters in *N. hemsleyana*'s aerial pitchers could have a profound effect on its function and allow it to occupy a hitherto unexploited niche.

MATERIALS AND METHODS

Over a period of eight weeks in May and June 2011, we measured 51 *N. hemsleyana* aerial pitchers within a lightly disturbed peat swamp and heath forest mosaic in western Brunei Darussalam at elevations between 20 and 50 m asl: at Badas, on the northern edge of the Badas Forest Reserve (4°4′N, 114°24′E), and Lumut, east of the Lumut pipeline road (4°38′N, 114°25′E). During the same period, we measured 42 aerial pitchers of *N. rafflesiana* at White Sands, a degraded heath forest with white, acidic sands (4°44′N, 114°35′E). Furthermore, between August 2011 and January 2012, we measured *N. hemsleyana* pitchers that had been occupied by bats in three additional sites within the same forest mosaic in western Brunei: Saw Mill (4°33′N, 114°29′E), Labi 31 (4°35′N, 114°30′E), and Labi 17 (4°30′N, 114°27′E). Some of these data have been published previously in Schöner *et al.* (2013). Following Schöner *et al.* (2013), we also captured *K. hardwickii* while pitchers were being monitored using harp traps.

We measured the length and orifice diameter of aerial pitchers of both *Nepenthes* species. Orifice diameter was taken as the average between the broadest point of the pitcher opening

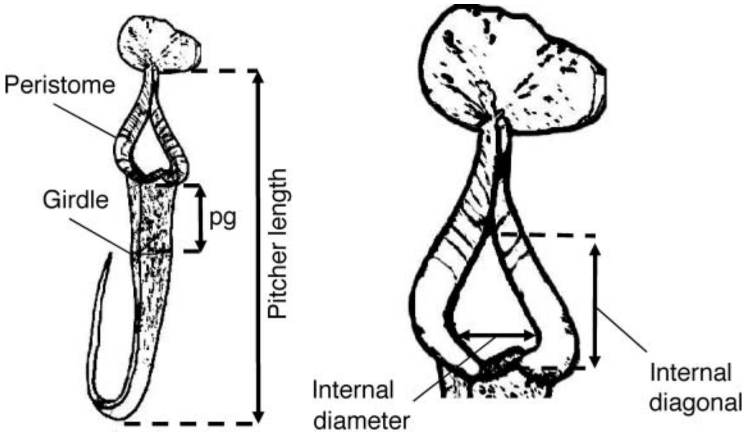

Fig. 1. Measurements undertaken of the aerial pitchers of *N. hemsleyana* and *N. rafflesiana* (pg = distance between peristome and girdle of *N. hemsleyana*; see text for details).

(internal diagonal) and the narrowest point of the pitcher opening (internal diameter) (Fig. 1).

In contrast to *N. rafflesiana*, the pitchers of *N. hemsleyana* have a girdle-like structure or hip that separates the pitcher into an upper, cylindrical section and a lower, more conical and tapered section (Fig. 1) (see Grafe *et al.*, 2011). Thus, to determine space available to bats, we measured the diameter of the pitcher at the girdle (girdle diameter), circumference of the pitcher at the girdle, and peristome–girdle length only for *N. hemsleyana*.

As a cone-shaped or tapered pitcher is likely to contribute to the bats' ability to wedge or stem themselves between the pitcher walls, we measured pitcher diameter at the orifice (DO) and pitcher diameter at the fluid level (DF). We calculated the ratio DF/DO as an index of the amount of taper in the part of the pitcher that is habitable to bats. The lower the value of this index, the higher the degree of tapering (a ratio of 1 = no tapering).

To estimate pitcher volume available to bats, we measured internal diameter, girdle diameter, and the lengths of the tapered and non-tapered zones of the pitchers. We calculated the total habitable space available to bats by assuming that pitchers could be reduced to cylinders and cones.

We measured the bats' body length and shoulder width to evaluate the fit between *K. hardwickii* and their roost. Although females were approximately 8% larger than males, females and males were pooled for the purposes of this study. Body length was measured as the distance between forehead and base of the tail wing membrane using a hand-held calliper ($n = 22$). We measured body width at shoulder height because this is the broadest and least compressible body part. Bats do not cling or hold on to the peristome but wedge themselves head first into the pitcher (Grafe *et al.*, 2011). To determine if bats fit comfortably into the pitcher without slipping into the digestive fluid, we measured the distance between peristome and fluid as well as the pitcher diameter at fluid height. We measured these variables in *N. hemsleyana* pitchers used by bats and in pitchers not known to be used by bats. The same measures were also taken for *N. rafflesiana* pitchers. All analyses were conducted with SPSS v.13 and Bias (v.8.2; epsilon-Verlag GbR 1989–2015). Descriptive statistics are given as means ± standard deviations.

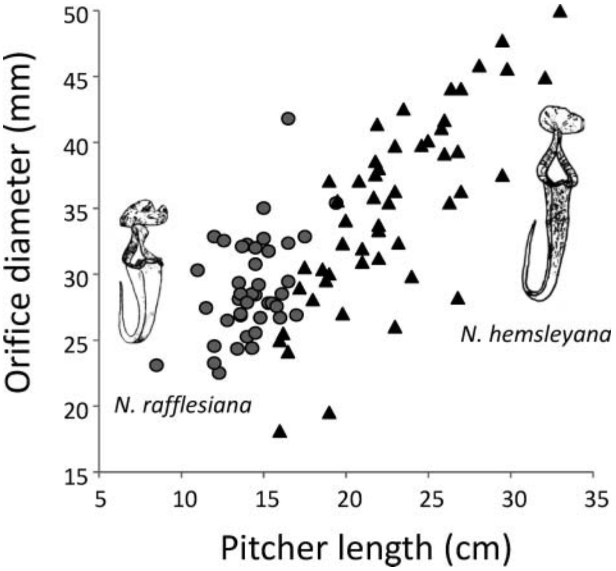

Fig. 2. Relationship between orifice diameter and pitcher length in *N. hemsleyana* (▲) and *N. rafflesiana* (●).

RESULTS

Pitcher length and orifice diameter

The aerial pitchers of *N. hemsleyana* were significantly longer than those of *N. rafflesiana* (Welch t-test: $t_{73} = 12.89$, $P < 0.001$; Fig. 2). Likewise, pitcher orifice diameter was larger in *N. hemsleyana* than in *N. rafflesiana* (Welch t-test, $t_{75} = 5.35$, $P < 0.001$) with higher variance (F-test: $F_{50,41} = 3.42$, $P < 0.001$; Fig. 2).

Tapering

Nepenthes hemsleyana pitchers are highly tapered between the peristome and the pitcher at fluid level (index = 0.37 ± 0.13, range = 0.06–0.74, $n = 51$). Tapering was significantly lower in *N. rafflesiana* (index = 0.56 ± 0.06, range = 0.47–0.66, $n = 42$) (Welch t-test, $t_{75} = 9.84$, $P < 0.001$).

Fluid volume and space availability

Median fluid volumes were significantly lower in *N. hemsleyana* (4.3 mL, range = 0–20.0 mL) than in *N. rafflesiana* (7.0 mL, range = 4.3–21.8 mL; Mann-Whitney U-test: $U = 313.5$, $n_1 = 37$, $n_2 = 37$, $P < 0.001$; Fig. 3). The conical space below the girdle (but above the fluid) in *N. hemsleyana* pitchers contributed considerably to the total habitable space. All *N. hemsleyana* aerial pitchers had girdle diameters above the average width of the bats at shoulder height (15.8 mm ± 1.4 mm; $n = 22$), suggesting that bats could manoeuvre into a part of the space below the girdle. Together with their respective calculated cylindrical

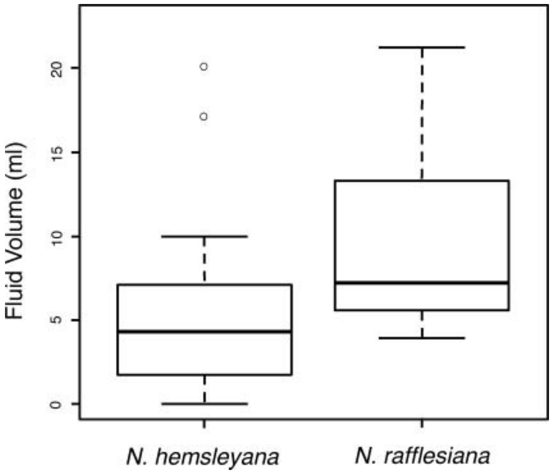

Fig. 3. Fluid volume in *N. hemsleyana* and *N. rafflesiana*. Boxes indicate the 25th and 75th percentiles, the line in the box represents the median, the whiskers are the 10th and 90th percentiles, and the dots show outliers.

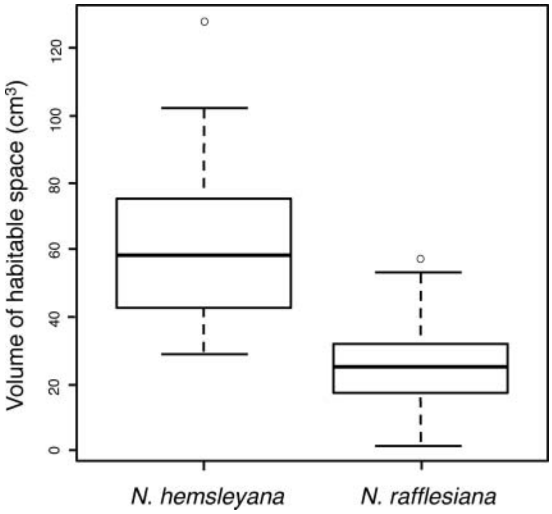

Fig. 4. Volume of habitable space in *N. hemsleyana* ($n = 23$) and *N. rafflesiana* ($n = 37$). See caption to Fig. 3 for further details.

volumes, the total habitable volume of 59.19 ± 25 cm^3 for *N. hemsleyana* pitchers averaged more than twice the habitable volume in *N. rafflesiana* pitchers (27.5 ± 13.25 cm^3; Welch *t*-test, $t_{75} = 6.43$, $P < 0.001$; Fig. 4). The distances between peristome and fluid were also significantly different between the two pitcher-plant species (Mann-Whitney *U*-test: $U = 86.5$, $n_1 = 42$, $n_2 = 72$, $P < 0.001$) with 97.2% of the *N. hemsleyana* pitchers having sufficient space to accommodate a single bat of average body length, compared with only 78.6% of *N. rafflesiana* pitchers (Fig. 5).

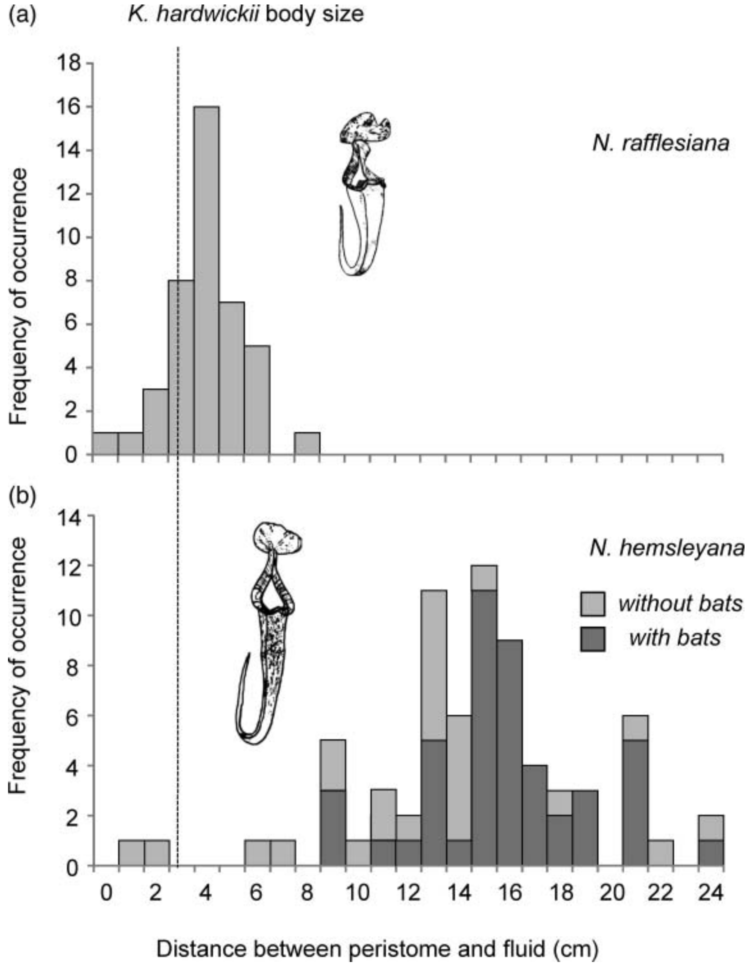

Fig. 5. Size distribution of aerial pitchers of (a) *N. rafflesiana* ($n = 42$) and (b) *N. hemsleyana* ($n = 46$) used as roosts by *K. hardwickii* (dark grey) and not seen to be used by bats ($n = 26$; light grey). Dashed line indicates the average body size of *K. hardwickii*.

Pitcher size relative to body size of *Kerivoula hardwickii*

The average body length of *K. hardwickii* was 32.6 ± 2.3 mm (range = 28.5–36.2 mm; $n = 18$; 14 females, 4 males; Fig. 5). Since *N. hemsleyana* aerial pitchers were strongly tapered below the girdle, the pitcher diameter at fluid level was significantly smaller than the shoulder diameter of *K. hardwickii* (Mann-Whitney *U*-test: $U = 100$, $n_1 = 22$, $n_2 = 17$, $P = 0.013$) (Fig. 6), allowing bats to wedge themselves between the pitcher walls well above the fluid. None of the pitchers with pitcher diameter above 22 mm at fluid level were used by *K. hardwickii* (Fig. 6). Pitchers known to have been used by bats had significantly smaller pitcher diameters at fluid level than pitchers not known to have been used as roosts (Mann-Whitney *U*-test: $U = 261$, $n_1 = 17$, $n_2 = 52$, $P = 0.011$). Pitcher diameter at fluid level was significantly larger in *N. rafflesiana* (Mann-Whitney *U*-test: $U = 523$, $n_1 = 52$, $n_2 = 42$,

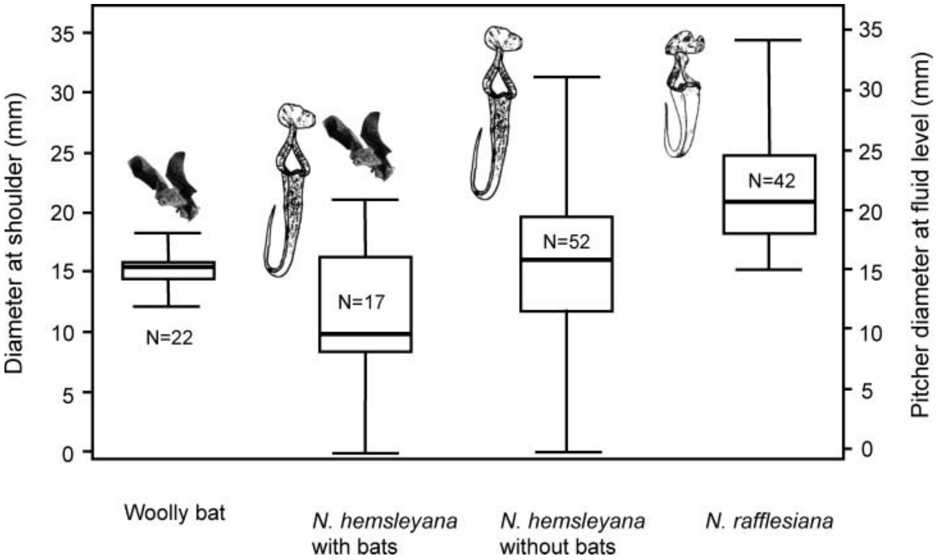

Fig. 6. Diameter of *K. hardwickii* at shoulder height versus pitcher diameter at fluid level in aerial pitchers of *N. hemsleyana* used by bats, aerial pitchers of *N. hemsleyana* not known to be used by bats, and in aerial pitchers of *N. rafflesiana* (photo of bat by C.C. Lee). See caption to Fig. 3 for further details.

$P < 0.001$) (Fig. 6), and, hypothetically, bats would slip into the fluid unless they were able to hold onto the edge of the peristome, thus exposing themselves to direct sunlight and potential predators.

DISCUSSION

Suitability of *N. hemsleyana* aerial pitchers as roosting sites for bats

This study identified a set of characteristics in *N. hemsleyana* that facilitate bat roosting. Particularly revealing are those traits that appear to be derived in *N. hemsleyana* and thus might have evolved to attract bats: low fluid levels, relatively large orifices, as well as the elongate, cylindrical, and basally strongly tapered pitchers.

The geometry of the *N. hemsleyana* aerial pitcher indicates that these pitchers are excellent roosting sites for *K. hardwickii*. The enlarged orifice in *N. hemsleyana*, created by the elongated rear pitcher wall, allows bats easier access to the pitcher interior. Once inside the pitcher, both the body length and body width of *K. hardwickii* are well matched to pitcher dimensions. The elongated, narrow pitchers provide sufficient space and appropriate morphology to accommodate individual bats well above the digestive fluid. We did not observe bats use as roosts pitchers that were wider than 22 mm at fluid level, suggesting selection on *N. hemsleyana* pitchers to either reduce fluid levels or to produce narrow, strongly tapering pitchers. Similarly, under conditions of few invertebrate species, the pitchers of several montane *Nepenthes* species produce pitchers that are highly adapted to the body size of *Tupaia montana*, whose feces are captured and digested by those pitcher plants (Chin *et al.*, 2010).

The dual strategy of *Nepenthes hemsleyana*

Although *N. hemsleyana* obtains about a third of its total foliar nitrogen from the feces or urine of *K. hardwickii* (Grafe *et al.*, 2011), the ability of its pitchers to trap insects, albeit reduced (Moran, 1996), suggests that *N. hemsleyana* follows a dual strategy of nitrogen acquisition. The orifice diameter of *N. hemsleyana* is significantly larger than that of *N. rafflesiana*, but it retains the ability to trap arthropod prey by aquaplaning when the peristome is wet [whether by rain, humidity or nectar (Bohn and Federle, 2004; Bauer *et al.*, 2009, 2011, 2015)]. The wettable peristome and the long waxy zone between the peristome and the girdle are nearly 100% effective in retaining prey that has fallen into the pitcher (Gaume and Di Giusto, 2009; Bauer *et al.*, 2011). Extra-floral nectaries along the inner rim of the peristome may also attract prey, although the rates of nectar production are much reduced compared with *N. rafflesiana* (Bauer *et al.*, 2011). Thus, the morphological traits of *N. hemsleyana*'s aerial pitchers compromise between attracting bats and capturing insects.

The adoption of a dual strategy is not unique to *N. hemsleyana. Nepenthes ampullaria* has also evolved to glean nutrients from trapping invertebrates and leaf litter that falls into its pitchers (Moran *et al.*, 2003; Pavlovič *et al.*, 2011). *Nepenthes rajah* and *N. macrophylla*, two species that attract small mammals, also show a combination of pitcher characteristics that serve dual functions of trapping arthropods and collecting feces (Chin *et al.*, 2010). In *N. lowii*, the dual strategy is divided between lower pitchers that trap insects and aerial pitchers that trap shrew feces (Clarke *et al.*, 2009). The retention of pitcher characters useful to capturing insects in *N. hemsleyana* suggests that the relative importance of the feces-trapping and carnivorous syndrome fluctuates temporally in their contributions to the plant's nitrogen demands. Alternatively, this could be a snapshot of ongoing evolutionary divergence, with some pitcher traits underlying genetic or developmental constraints that prevent it from completely abandoning highly conserved trap structures such as the peristome.

Evidence from morphological and molecular phylogenetic studies indicates that a long, cylindrical waxy zone in upper pitchers is a basal feature (Bauer *et al.*, 2012). As such, the partly cylindrical, funnel-shaped aerial pitcher of *N. hemsleyana* was most likely pre-adapted and later modified to accommodate roosting bats leading to a functional divergence away from the typical arthropod-trapping strategy. Our results thus support the notion that slight allometric differences in pitcher morphologies facilitate divergence to new ecological niches and nitrogen sequestration strategies (Gaume and Di Giusto, 2009; Chin *et al.*, 2010; Bauer *et al.*, 2011; Bonhomme *et al.*, 2011b; Grafe *et al.*, 2011; Greenwood *et al.*, 2011).

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