

# Handle with care: enlarged pads improve the ability of Hardwicke's woolly bat, *Kerivoula hardwickii* (Chiroptera: Vespertilionidae), to roost in a carnivorous pitcher plant

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Many animals including several foliage-roosting bats have evolved adhesive pads, which facilitate clinging to and moving on smooth surfaces. In South-East Asia, Hardwicke's woolly bat (*Kerivoula hardwickii*) roosts in furled leaves of different Zingiberales plants and in pitchers of carnivorous *Nepenthes* species. This roosting behaviour led to a mutualism with *Nepenthes hemsleyana*, which provides high-quality roosts in exchange for nitrogen-rich bat faeces. However, even small injuries in the soft pitcher tissue of *N. hemsleyana* lead to accelerated wilting and make pitchers unavailable within days. As occupied pitchers were never injured by bats, we hypothesized that bats roosting in such sensitive plant tissue have evolved pads that enable them to cling to and move inside their roosts without using their claws. We found that *K. hardwickii* has proportionately larger thumb and foot pads and more effectively adheres to smooth surfaces than closely related *Kerivoula* species that roost under wilted foliage and – contrary to our prediction – compared to *Myotis muricola* that also roosts in furled leaves. In conclusion, enlarged pads of *K. hardwickii* could not only facilitate clinging to slippery plant roosts but also prevent damage to delicate plant tissue of their mutualism partner *N. hemsleyana*.

ADDITIONAL KEYWORDS: animal–plant interaction – Borneo – foliage roosting – foot pad – *Kerivoula* – mutualism – *Myotis muricola* – *Nepenthes* – roosting ecology – skin adhesion.

## INTRODUCTION

The capability to move on slippery surfaces is widespread in animals such as arachnids, insects, amphibians and reptiles (Federle *et al.*, 2002; Peattie *et al.*, 2011; Endlein & Barnes, 2014). In contrast, only a few mammals, for example the feathertail glider *Acrobates pygmaeus* Shaw, 1793 (Rosenberg & Rose, 1999; Riskin & Racey, 2010), have evolved adhesive pads to facilitate that task. In bats, pad-like structures on the thumbs and feet have presumably evolved independently in the genera *Thyroptera*, *Myzopoda*, *Neoromicia* and in the common ancestor of *Tylonycteris* and *Glischropus* (Thewissen & Etnier, 1995). The mechanisms how these pads work

can be quite different (Endlein & Barnes, 2014). While the bat species *Thyroptera tricolor* Spix, 1823 makes use of dry adhesion via suction disks (Riskin & Fenton, 2001), pads of *Myzopoda aurita* Milne-Edwards & A. Grandidier, 1878 adhere to the surfaces of their plant roosts via wet adhesion (Riskin & Racey, 2010). Most bat species with adhesive pads live in slippery, living plant structures (Kunz & Fenton, 2005; Feng, Li & Wang, 2008; Chaverri, Gillam & Vonhof, 2010; Ralisata, Rakotondravony & Racey, 2015). However, it is often unclear whether and how these pads facilitate roosting in those plants (Riskin & Fenton, 2001; Riskin & Racey, 2010), as can be seen in *Neoromicia nanus* Peters, 1852 (Thewissen & Etnier, 1995). Interestingly, other foliage-roosting bat species, such as tent-making bats, have not evolved adhesive pads and only use their claws to cling to plant structures (Kunz & Fenton, 2005).

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The South-East Asian bat species *Kerivoula hardwickii* Horsfield, 1824 roosts in developing furled leaves of different ginger (Zingiberaceae), banana (Musaceae) and aroid (Araceae) species (McArthur, 2012; M. G. Schöner, C. R. Schöner, pers. observ.), which are available as roosts only for a few hours or days before the leaves unfurl (Happold & Happold, 1996; M. G. Schöner, C. R. Schöner, pers. observ.). On Borneo, *K. hardwickii* additionally roosts in pitcher-shaped trapping organs of three carnivorous pitcher plant species, *Nepenthes ampullaria* Jack, 1835, *Nepenthes bicalcarata* Hook.f., 1873 and *Nepenthes hemsleyana* Macfarl., 1908 (Grafe *et al.*, 2011; McArthur, 2012; Schöner *et al.*, 2013, 2016). Only with *N. hemsleyana*, the bat interacts mutualistically by receiving a parasite-free roost with beneficial microclimate for fertilizing the plants with nitrogen-rich faeces (Schöner *et al.*, 2013, 2017). *Nepenthes hemsleyana* additionally facilitates the mutualism, for example, with a pitcher shape that prevents the bats from falling into the digestive liquid or an echo-reflecting structure, which can easily be detected by the bats (Schöner *et al.*, 2013, 2015b; Lim *et al.*, 2015; Schöner, Simon & Schöner, 2016). However, it has never been investigated whether traits of *K. hardwickii* also facilitate roosting in funnel-shaped plant structures including pitchers of their mutualism partner *N. hemsleyana*.

Due to their low lignin content, *N. hemsleyana* pitchers are very sensitive to damage (Osunkoya, Daud & Wimmer, 2008). Intact *N. hemsleyana* pitchers usually last for around 90 days (Schöner *et al.*, 2015a). In contrast, pitchers, which we had injured involuntarily, completely wilted and crumpled within only 7 days and were no longer accessible for the bats (M. G. Schöner, C. R. Schöner, pers. observ.). Moreover, the plants need 2.5 months on average to produce a new pitcher (Schöner *et al.*, 2015a). Because of their fragility and rarity (Schöner *et al.*, 2015b), *K. hardwickii* should handle their roosts with care. Previous studies already showed that roosting bats do not injure the soft tissue of *N. hemsleyana* pitchers or reduce their longevity (Schöner *et al.*, 2015a). Similarly, Neotropical tent-roosting bats modify their leaf roosts in a way that water supply inside the leaves is maintained. The leaf roosts are longer available for the bats and rather inconspicuous for potential predators (Cholewa *et al.*, 2001).

We hypothesized that there should be a high selection pressure on *K. hardwickii* to avoid injuries of their host plants while moving and roosting inside. If so, *K. hardwickii* (1) should have morphological structures that potentially enable adhesion to smooth surfaces and (2) should be able to cling to and move on smooth surfaces without using their claws. We predicted that species with similar roosting habits as *K. hardwickii* should have similar morphological structures and

sticking abilities, while such traits should be missing in bat species with different roosting ecology even if they are closely related to *K. hardwickii*.

## METHODS

### DESCRIPTION OF STUDY SITE AND TIME

Fieldwork and experiments took place in the Belait district of Brunei Darussalam and the Mulu National Park of Sarawak/Malaysia from 14 August 2011 to 14 January 2012, from 20 June 2012 to 3 December 2012, from 14 April 2014 to 1 September 2014 and from 7 to 25 February 2016.

During each of these field seasons, we caught individuals of the species *K. hardwickii*. For comparisons, we additionally caught individuals of the closely related *Kerivoula intermedia* Hill & Francis, 1984 and *Kerivoula pellucida* Waterhouse, 1845 (Khan *et al.*, 2010; Hasan & Abdullah, 2011), which roost in wilted plant structures as well as individuals of the not closely related species *Myotis muricola* Gray, 1846 that – similarly to *K. hardwickii* – uses furled banana leaves as roosts (Pottie *et al.*, 2005; Francis & Barrett, 2008; Phillipps & Phillipps, 2016; M. G. Schöner, C. R. Schöner, pers. observ.). We caught bats with harp traps (see Schöner *et al.*, 2013) and additionally searched for *K. hardwickii* and *Myo. muricola* in *Nepenthes* pitchers and in furled leaves of ginger (*Alpinia ligulata* K.Schum., 1899; *Boesenbergia grandis* R.M.Sm, 1982), banana (*Musa muluensis* M.Hotta, 1967) and aroid plants. We determined sex, forearm, thumb and toe length of all captured bats. For experiments and further analysis, we only used adult non-pregnant or non-lactating individuals. We marked all individuals with a sterile biopsy punch (Stiefel Laboratories, Offenbach Germany; diameter: 2 mm) at their wing membrane to recognize recaptures and marked *K. hardwickii* with transponders (ISO 11784/11785; Paddy-Mark, UK; see Kerth & König, 1999) for long-term identification. Bats kept for experiments were placed at room temperature in humid bags to prevent dehydration, fed with water and mealworms and released within 12 h after capture into their original habitat. All procedures performed with bats adhered to the Animal Behaviour Society ([Guidelines for the treatment of animals in behavioural research and teaching, 2012](#)) and were in accordance with the ethical standards of the University Brunei Darussalam Research Committee and the Forestry Department Sarawak that gave permission to capture and handle the bats.

### DETERMINATION OF PAD SIZE

We placed ten *K. hardwickii* in Falcon tubes (diameter: 3.0 cm, length: 11.5 cm) that have a similar diameter

compared to *N. hemsleyana* pitchers ( $4.53 \pm 0.85$  cm; see Schönner *et al.*, 2013) to find out which body parts are relevant for moving on and clinging to the slippery surface. We compared the extremities of *K. hardwickii* (forearm length 28.5–35.1 mm) to that of the sympatric and similar-sized *K. intermedia* (forearm length 26.6–30.1 mm), *K. pellucida* (forearm length 26.3–33.3 mm) and *Myo. muricola* (forearm length 33.3–36.3 mm; Table 1; Francis & Barrett, 2008; Khan *et al.*, 2010; Hasan & Abdullah, 2011).

As *K. hardwickii* adhered to the tube surface with their thumb and foot pads, we took pictures of these structures from above (with a 90° angle between forearm and thumb or in a 90° angle to the camera; Fig. 1) from all focal bat species. To calculate the pad area, we used ImageJ (Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, MD, USA, <http://imagej.nih.gov/ij/>, 1997–2014). With this software, we first marked thumbs/toes with a line in the pictures whose exact length was known from the earlier measurements of the referring individual. This defined line was used as scale. Then, we marked the areas of the thumb and foot pads (Fig. 1) with the freehand or the polygon tool, and ImageJ automatically analysed the size of the area.

#### SLIDING EXPERIMENT

To find out how effective the four bat species' thumb and foot pads are for clinging to a smooth surface, we conducted a sliding experiment (Table 1) for which we placed the bats again in Falcon tubes that we horizontally fixed in a self-built rotation device. We ensured that the Falcon tubes and bats were dry as humidity could influence adhesion effects. Moreover, we only tested bats that rested calmly in the tube (see Table 1). Before each trial, we checked if the foot and thumb pads of the bats were fully attached to the surface of the Falcon tube. Due to the smooth and hard surface of the tube and its lid, the bats could not use their claws to interlock to the surface. The rotation device automatically stopped at angles of 30°, 60° and 90° and continued after 5 s. We filmed each experiment (Sony

HDR-CX560VE) to determine the angle at which bats started to slide.

Finally, we compared the pad sizes and sliding angles of *K. hardwickii* individuals roosting in pitchers to those roosting in furled leaves (we only used individuals that we had found in their roosts and not in harp traps).

#### DATA ANALYSIS

We captured 304 bats of the four focal species. Some of these bats were so agitated that the quality of the photographs and the video was insufficient for measuring their thumbs and feet. Students without background knowledge of the hypotheses analysed the photographs and videos. To correct for slight body size differences of the different bat species or sexes, we calculated an individual's 'relative pad size' using the following formula:

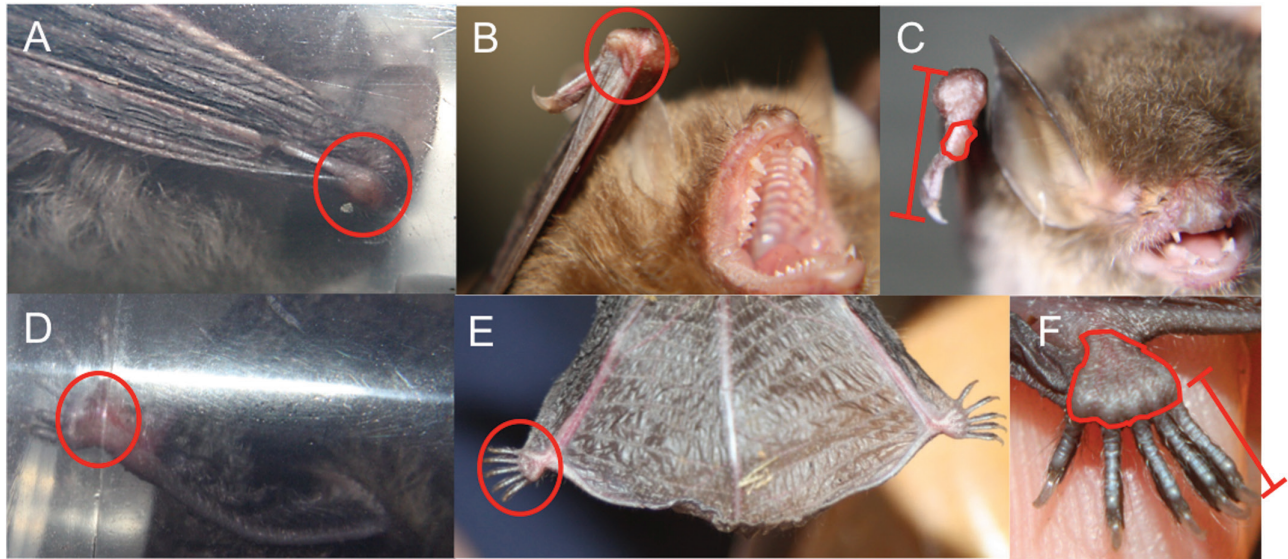
$$\text{Relative pad size} = \frac{\text{absolute pad size}(\text{mm}^2)}{\text{forearm length}(\text{mm})}$$

We used Monte Carlo tests to test the null hypothesis that the affiliation to a certain species does not affect relative pad size or sliding angle of the bats during the experiment. We first calculated each species' mean relative pad size/sliding angle, which we then compared to the distribution of values expected under the null hypothesis. The null hypothesis distribution was obtained by permuting the relative pad sizes/sliding angles between species and then calculating the mean relative pad size/sliding angle per species. This procedure was repeated 10 000 times from which the null distribution of the mean relative pad size/sliding angle was obtained. We calculated the *P*-value by comparing the mean relative pad size/sliding angle for the considered species to the null distribution. We applied the same Monte Carlo test to find intraspecific differences in pad size and sliding angle of *K. hardwickii* individuals roosting in pitchers and those roosting in furled leaves. To compare the different bat species regarding their abilities to avoid sliding, we used Fisher's exact tests for count data.

**Table 1.** Number of individuals whose pad size was measured and those bats that were tested in the sliding experiment

Species	Thumb pad			Foot pad			Sliding experiment		
	♂♂	♀♀	Σ	♂♂	♀♀	Σ	♂♂	♀♀	Σ
<i>Kerivoula hardwickii</i>	45	61	106	59	77	136	39	53	92
<i>Kerivoula intermedia</i>	23	28	51	24	27	51	9	5	14
<i>Kerivoula pellucida</i>	15	10	25	12	11	23	4	4	8
<i>Myotis muricola</i>	3	6	9	3	6	9	3	6	9





**Figure 1.** Thumb (A–C) and foot pads (D–F) measured for morphological comparison. As can be seen when placed in a Falcon tube (A, D), *Kerivoula hardwickii* attach to surfaces with thumb (B) and foot (E) pads. To measure the size of these pads (C, F), we used the lengths of the thumbs and toes (indicated by lines) for calibration and then calculated the pad sizes (indicated by polygons).

## RESULTS

### INTERSPECIFIC COMPARISON OF PAD SIZES AND SLIDING ANGLES

All tested individuals were in close contact with the tube's surface. We found that *K. hardwickii* did not have to use their claws to stick to the surface of the Falcon tubes. Instead, all individuals automatically postured their ankles and wrists in angles so that the bats' claws only slightly touched the surface while the thumb and feet pads stuck to the tube's surface (Fig. 1A, D). The relative pad size of thumbs and feet were significantly larger in *K. hardwickii* than expected by random distributions of the relative pad sizes of all species. In all other tested species, the relative thumb and foot pad size was smaller than expected (Fig. 2A, B).

The different morphology is also reflected in different capabilities of the focal bat species to stick to the Falcon tube. Of all tested individuals of *K. hardwickii*, 82.6% did not slide at all. This significantly differed from *K. intermedia* and *K. pellucida* where only a minority of individuals (28.6 and 37.5%, respectively) could avoid sliding at angles between 0° and 90° (Fig. 2C). Astonishingly, 91.7% of all *Myo. muricola* individuals slid. Consequently, *Myo. muricola* and *K. hardwickii* differed most in their abilities to avoid sliding in the Falcon tube (Fisher's exact test for count data to compare all species:  $P < 0.001$ ; for post hoc analysis, see Fig. 2C) although both species roost in furled leaves. Finally, *K. hardwickii* slid at significantly steeper angles than the other three tested bat species (Fig. 2D).

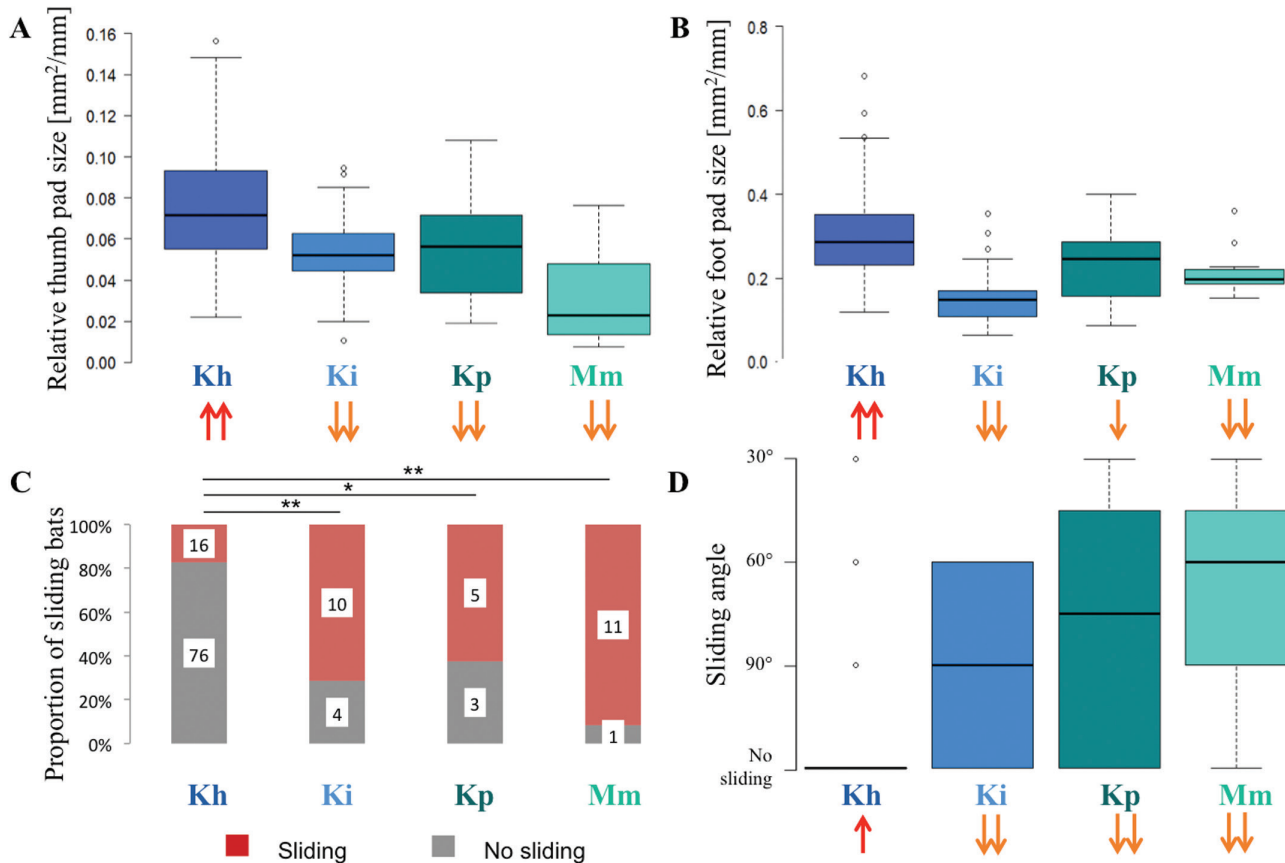
### INTRASPECIFIC COMPARISON OF *K. HARDWICKII* ROOSTING IN PITCHERS VS. FURLED LEAVES

Individuals of *K. hardwickii* roosting in furled leaves had significantly smaller relative foot pad sizes ( $N = 45$ , median =  $0.27(\text{mm}^2/\text{mm})$ , range =  $0.12 - 0.54(\text{mm}^2/\text{mm})$ ) compared to those bats using pitchers ( $N = 91$ , median =  $0.30(\text{mm}^2/\text{mm})$ , range =  $0.13 - 0.68(\text{mm}^2/\text{mm})$ ,  $P < 0.001$ ). In contrast, the relative thumb pad size of individuals roosting in pitchers ( $N = 72$ , median =  $0.07(\text{mm}^2/\text{mm})$ , range =  $0.02 - 0.13(\text{mm}^2/\text{mm})$ ) did not differ from that of those bats using furled leaves ( $N = 34$ , median =  $0.07(\text{mm}^2/\text{mm})$ , range =  $0.03 - 0.16(\text{mm}^2/\text{mm})$ ,  $P = 0.63$ ). The difference in the relative foot pad size did not influence the bats' performance in the sliding experiment in which the vast majority of individuals very well attached to the slippery surface regardless of where we had found them roosting (for both individuals roosting in furled leaves and those roosting in pitchers: median sliding angle =  $61^\circ - 90^\circ$ , range =  $0^\circ - 90^\circ$ , respectively,  $P = 0.53$ ).

## DISCUSSION

### MORPHOLOGICAL PAD STRUCTURES IN THE FOCAL BAT SPECIES

Compared with closely related species, *K. hardwickii* has enlarged thumb and foot pads, which apparently help the bat to cling to the roosts' surface without using its claws. The closely related species



**Figure 2.** Results of morphological measurements and sliding experiments. A, relative thumb and (B) relative foot pad sizes of different species (see text for details). C, interspecific comparison of the proportions of sliding and not sliding bats. The category ‘sliding’ comprises all bats that slid irrelevant of the angle. Fisher’s exact tests for count data were applied to test whether the proportion of *Kerivoula hardwickii* starting to slide was smaller than that of the other species (significance level: \* $P < 0.05$ ; \*\* $P < 0.01$ ). There was no difference between the proportions of sliding individuals between the other species (Ki vs. Kp:  $P = 1$ ; Ki vs. Mm:  $P = 0.13$ ; Kp vs. Mm:  $P = 0.08$ ). All significances remained after a sequential Bonferroni correction. D, angles where bats of different species started to slide. Significant positive (↑) or negative (↓) differences of sliding levels from random distributions (Monte Carlo tests) are shown below each boxplot: significance level: ↑, ↓:  $P < 0.05$ ; ↑↑, ↓↓:  $P < 0.01$ . Kh, *Kerivoula hardwickii*; Ki, *Kerivoula intermedia*; Kp, *Kerivoula pellucida*; Mm, *Myotis muricola*.

*K. intermedia* and *K. pellucida* had smaller thumb and foot pads relative to their body size, which could explain why these bats started sliding at shallower angles during the sliding experiment. Contrary to our predictions, *Myo. muricola* had both the smallest relative thumb pads and the worst ability to adhere to the smooth surface of the Falcon tubes in the sliding experiment although this species roosts in furled leaves as well. Only one of 12 tested individuals stayed attached to the surface of the plastic tube at a 90° angle.

Currently, it is unclear how exactly *K. hardwickii*’s pads function. In contrast to *Myo. muricola*, which cling to furled banana leaves by mechanical interlocking via their claws, it is likely that *K. hardwickii* uses bonding mechanisms to adhere to their roost. Bonding can

be realized via Van der Waals forces, which are common in dry adhesion but only work at distances of a few nanometres (Endlein & Barnes, 2014). As *K. hardwickii* does not have suction discs that could maintain such forces, wet adhesion, which could be achieved via sweat glands, seems to be more likely.

A likely explanation why *K. hardwickii* does not have pads that are as sophisticated as those of the bat species *T. tricolor* and *Myz. aurita* is that the interaction between the latter two species and their host plants is much older than that between *K. hardwickii* and its plant interaction partners. Schliemann (1971) suggested a gradual and long-lasting evolutionary process that has led to the evolution of highly developed adhesive pads in *T. tricolor* and *Myz. aurita*. In contrast, the interaction between *K. hardwickii* and the

pitcher plants is probably very young as the diversity of *Nepenthes* derives from a recent adaptive radiation after the last glacial period (Clarke, 2006; Meimberg & Heubl, 2006; Chin, Moran & Clarke, 2010).

#### KERIVOULA HARDWICKII'S ENLARGED PADS ARE BENEFICIAL TO BOTH BATS AND PITCHER PLANTS

In contrast to, for example, leaves of *Heliconia* that are able to maintain water supply of the lamina even after modification by plant-roosting bats (Cholewa *et al.*, 2001), *N. hemsleyana* become unavailable for *K. hardwickii* within days after injury. The presence of enlarged pads in *K. hardwickii* probably was an important prerequisite for the successful establishment of the mutualism with *N. hemsleyana*.

It is unlikely that the enlargement of the pads is a result of coevolution with the pitcher plants as roosting in furled leaves is probably more widespread and older than roosting in *Nepenthes* pitchers that is so far only known from Northern Borneo (Clarke, Moran & Lee, 2011; Grafe *et al.*, 2011). Nevertheless, microevolutionary processes might play a role as indicated by the increased foot pad size of *K. hardwickii* individuals roosting in *Nepenthes* pitchers compared to those roosting in furled leaves. Such microevolutionary adaptations enable organisms to deal with new environments within relatively short time frames (Hendry & Kinnison, 2001). Thus, larger foot pad structures may benefit bats in areas with high pitcher plant densities. However, during the sliding experiment, all individuals strongly adhered to the smooth surface of the tube irrespective of their original roost probably because the ranges of their foot pad sizes still broadly overlap. Future research should investigate why relatively larger pad structures in *K. hardwickii* roosting in pitchers could be advantageous, for example, by investigating the locomotion of bats with different pad sizes.

#### THE FUNCTION OF ADHESIVE CAPABILITIES IN INTERSPECIFIC INTERACTIONS

Mutualistic interactions are drivers of evolution and often result in morphological adaptations of the involved partners. For example, the proboscis of long-tongued flies (*Prosoeca ganglbaueri*) strongly correlates with the corolla of its primary foot plant *Zaluzianskya microsiphon* but vary among sites (Anderson & Johnson, 2007). In the context of mutualism, adhesion capabilities have rarely been investigated. One example can be seen in ants of the genus *Crematogaster* that can move on the highly slippery waxy layer of *Macaranga* spp., while other ants are excluded. This helps the plants to only host mutualistic

ant species, while at the same time benefiting their ant partners by reduced competition with other ant species (Federle *et al.*, 1997; Whitney & Federle, 2013). Such evolutionary processes can not only be seen in mutualisms but also in other types of interspecific interactions, including parasitism. The southern green stink bug *Nezara viridula*, for example, evolved adhesion mechanisms that improve the attachment to its host plant *Vicia faba*. However, many questions on the function of adhesion capabilities remain.

This is especially true regarding bat–plant interactions: first, if bats can simply stick to plant surfaces such as furled leaves via interlocking – as it is the case for *Myo. muricola* – why have several species evolved adhesive pads? When is the use of such pads on slippery plant structures more advantageous than the use of claws? Do other species than *K. hardwickii* as well need to mitigate damage to their plant interaction partner? Apart from investigating the proximate mechanisms of adhesive structures, answering these questions will give insights into the ultimate function of morphological traits for interspecific interactions.

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