



Low costs reinforce the mutualism between bats and pitcher plants



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ABSTRACT

Whether mutualisms persist or vanish during the course of evolution depends on the cost-benefit ratio for the species involved. In the interaction between the pitcher plant *Nepenthes hemsleyana* and the bat *Kerivoula hardwickii* both partners mutually benefit: *N. hemsleyana* offers high quality roosts in exchange for nutrients from the bats' faeces. Here, we tested the hypothesis that the partners should also incur costs from their interaction. In the field, we examined potential costs that are likely to occur in our system and that are already known to be present in other bat-plant interactions. Regarding the plants, the bats could injure the tissue of the fragile pitchers and thus affect the pitchers' longevity. Regarding the bats, the ephemeral nature of *N. hemsleyana* pitchers and incoming rainwater could force them to switch these roosts more frequently than if using an alternative roost type. Our results suggest that neither the pitcher plants nor the bats accrue substantial costs from their interaction. We conclude that the ratio of high benefits to low costs strengthens this mutualism and promotes reciprocal adaptations and specialisations.

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1. Introduction

Mutualisms are key interactions in nature that occur in all ecosystems (Bronstein, 1994 and Bronstein, 2001). To maintain a mutualism, benefits gained by the species must outweigh the costs, otherwise the partners become autonomous again or one partner parasitises the other (Sachs and Simms 2006). For a full understanding of the ecology and evolution of mutualisms, the evaluation of both benefits and costs is therefore important (Bronstein, 2001). However, because costs in mutualisms are difficult to identify and in particular to quantify they are less studied than the benefits (Bronstein, 2001).

Carnivorous plants occur in nutrient-deprived habitats and typically compensate the lack of nutrients by capturing arthropods (Givnish et al., 1984). However, the pitcher plant *Nepenthes hemsleyana* (Macfarlane, 1908) is an inefficient arthropod trap catching seven times less prey than closely related species (Moran, 1996). Instead of capturing large amounts of arthropods, the plant attracts and hosts bats of the species *Kerivoula hardwickii* (Horsfield, 1824)

in its pitchers whose faeces contribute substantially to the plant's foliar nitrogen (Grafe et al., 2011). *N. hemsleyana* is the only known pitcher plant species that benefits from bats. Occasionally, the bats use other *Nepenthes* (Linnaeus, 1753a) species (*Nepenthes bicalcarata* (Hooker, 1873), *Nepenthes ampullaria* (Jack, 1835)) but only if their pitchers are damaged or dead. Intact pitchers of these species contain too much digestive fluid to allow bats to roost in them (Schöner et al., 2013).

The bats profit from roosting in *N. hemsleyana* pitchers because those pitchers are roosts of higher quality than the damaged or dead pitchers of the other two *Nepenthes* species. Only *N. hemsleyana* pitchers provide the bats with a stable microclimate with respect to humidity, which is more variable inside *N. bicalcarata* and *N. ampullaria* pitchers. Moreover, bats roosting in the latter species are exposed to a higher parasite infestation risk. Only bats roosting in *N. hemsleyana* pitchers are free of parasites that depend on the bats' roost for reproduction (Schöner et al., 2013 and Schöner, unpublished data).

Currently, nothing is known about whether *N. hemsleyana* and *K. hardwickii* also incur costs from their interaction. Potentially, a variety of different costs would be possible. For example, bats could reduce *N. hemsleyana*'s arthropod capture rate when blocking the pitchers' entrance. The bats themselves may suffer from an increased predation risk when they use weakly pigmented pitchers because they are more visible from outside. Here, we investigated if

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factors that have already been shown to be costly in other bat–plant interactions also negatively affect either the bats or the pitcher plants in the currently studied mutualism.

Firstly, we wanted to test the hypothesis that *K. hardwickii* injure the pitchers with their claws when they enter or leave these roosts. From some other bat species it is known that they modify and damage the plant material they are roosting in (Kunz and McCracken, 1996). *N. hemsleyana* pitchers have a low lignin content (Osunkoya et al., 2008), thin walls and are very delicate. Thus, bat occupancy could decrease the pitchers' longevity.

Secondly, roosting in *N. hemsleyana* pitchers may also accrue costs for *K. hardwickii*. We hypothesised that the bats have to regularly invest considerable time in finding new and suitable *N. hemsleyana* pitchers, which then only provide short-lived roosts. Locating highly ephemeral roosts is a challenging task for bats, as has been shown for example in *Thyroptera tricolor* (Spix von, 1823) (Chaverri et al., 2010). *N. hemsleyana* pitchers collapse when they start senescing after a lifespan of a few weeks (Osunkoya et al., 2008). In contrast, the dead pitchers of *N. bicalcarata* and *N. ampullaria* are not only more abundant than the rare *N. hemsleyana* pitchers but they also maintain their shape because of their high lignin content (Osunkoya et al., 2008 and Schöner et al., 2013). Thus, bats should have to invest more energy for searching for suitable *N. hemsleyana* roosts than for the less suitable dead pitchers of *N. bicalcarata* and *N. ampullaria*, which we expected to be longer lasting. Additionally, it is unknown so far if *N. hemsleyana* pitchers are continuously provided at the same plant like in the case of *N. bicalcarata* and *N. ampullaria* plants. *N. bicalcarata* and *N. ampullaria* plants used by *K. hardwickii* always contain one to 30 additional habitable roost pitchers. In contrast, *N. hemsleyana* plants rarely offer more than four pitchers to the bats (personal observation).

Moreover, we hypothesised that heavy rainfall could temporarily fill up *N. hemsleyana* pitchers with water. Pitchers of this species are usually completely intact when used by the bats, and without holes in the bottom. This would lead to further costs for *K. hardwickii* using *N. hemsleyana* pitchers as incoming water could expel bats from their current roost immediately. If such an emergency event happens during daylight hours and in rainy conditions, the bats' predation risk and energy loss would be increased (Rydell et al., 1996 and Voigt et al., 2011).

Assessing these potential costs for the involved partners and the resulting cost-benefit ratio will shed light on the interaction strength in the mutualism between *N. hemsleyana* and *K. hardwickii*.

2. Methods

Field studies were conducted at three sites (referred to here as “Labi”, “Saw Mill”, “Badas”) in the Belait district/Brunei Darussalam from 20 June to 3 December 2012 and from 14 April to 1 September 2014.

To determine whether bats damage the pitcher tissue and thus shorten the pitchers' longevity, we monitored 25 *N. hemsleyana* pitchers from the day they opened their lid until they started to decay and could no longer be occupied as the pitchers collapsed. Pitchers were checked daily for roosting bats. After the bats had left the pitchers we visually inspected if they had injured the inner pitcher tissue and/or peristome. With a Welch Two Sample *t*-test we tested whether pitchers occupied or not occupied by bats differ in their longevity. We computed a Pearson's product-moment correlation to investigate if the time period pitchers are occupied by bats negatively correlates with the pitchers' longevity.

The above-described measurements also provided data about how long *N. hemsleyana* pitchers in general are suitable roosts for bats. We additionally tested the hypothesis that any given plant of *N. hemsleyana* has at least one pitcher that is suitable for *K. hard-*

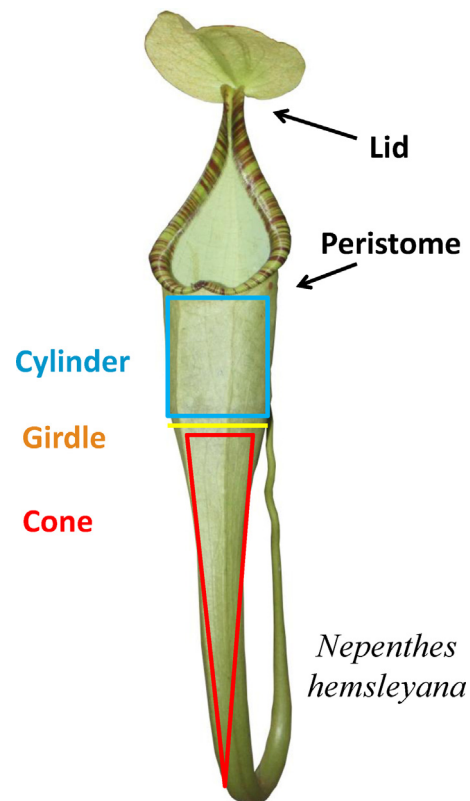


Fig. 1. Morphology of a *N. hemsleyana* pitcher.

wickii as a roost at any given time. Every day we monitored the 25 *N. hemsleyana* plants from 20 June to 3 December 2012 and checked if at least one pitcher is available for the bats to roost in. We investigated if the amount of plants that continuously provides pitchers differs from that with intermittent pitcher production using a Chi-squared test for given probabilities. We also determined how long the monitored *N. hemsleyana* plants did not offer a suitable pitcher to the bats. Moreover, we investigated how long it takes until a pitcher fully develops and if the development is completed before older pitchers of the same plant decay. Thus, we measured the time period from the day a pitcher opened its lid until the next pitcher of the same plant opened its lid. With a paired *t*-test we tested if the time *N. hemsleyana* plants need to produce new pitchers differs from the time periods the preceding pitcher is suitable as a bat roost.

To find out how long *N. bicalcarata* and *N. ampullaria* pitchers can be used by the bats, we marked 48 *N. bicalcarata* and 40 *N. ampullaria* pitchers that had already lost their digestive fluid and had just started to senesce in July 2012. We checked their condition in November 2012 (after four months) and again in April and August 2014 (after 21 and 25 months). We assumed that *N. bicalcarata* and *N. ampullaria* pitchers stop being suitable bat roosts when pitchers fell off the plants or when the bottom of the pitchers was destroyed. With Pearson's Chi-squared tests we compared if there were interspecific differences in the pitchers' suitability as bat roost after an observation period of four months.

Bats mainly use the cylindrical space above the girdle of *N. hemsleyana* pitchers for roosting (Grafe et al., 2011) (Fig. 1). If the fluid level reaches this roosting space, the bats are forced to search for a new roost. To find out if rainwater regularly floods *N. hemsleyana* pitchers, we checked and counted all *N. hemsleyana* pitchers after heavy rain in the three study sites in July and November 2012. We noted when the fluid level reached the pitcher's girdle. Moreover, we determined the canopy cover above the pitchers with a spher-

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