The Secrets of Night-Blooming Bromeliads and Bats

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Introduction

Unlike working with plant species that open their flowers during the day, studying night-blooming bromeliads requires extensive field work under poor visibility conditions. The nocturnal ("night-shift") pollinators, including bats and moths, are very different in behavior and biology in comparison to their diurnal ("day-shift") counterparts, such as hummingbirds and bees (i.e., different physiological needs, attraction to different floral traits, duration of visits; Willmer 2011). Furthermore, the need for special equipment to record nocturnal pollination may explain why night-blooming bromeliads are less studied than the day-blooming species.

Among angiosperms, bromeliads are remarkable for their floral biology, since most of the species appear to be primarily pollinated by vertebrates, rather than insects (Krömer et al. 2006). Most other animal-pollinated plants, including the orchids, are pollinated largely by insects. In the Neotropics, where almost all bromeliad species occur, hummingbirds and bats are the most important vertebrate pollinators (Fleming et al. 2005). Hummingbirds are the most frequently reported bromeliad-pollinators (Kessler & Krömer 2000; Carranza-Quiceno & Estévez-Varón 2008), resulting in a ratio of up to 20 bird-pollinated ("ornithophilous") to one bat-pollinated ("chiropterophilous") species (Sazima et al. 1999). Here, we present a brief overview of the knowledge about bat-pollination in Bromeliaceae, with special focus on a recent study carried out by our own working group.

Bat-Pollination Syndrome

In general, animal pollination syndromes are sets of floral characteristics that are shared by unrelated plant species that are pollinated by a particular kind of animal. The main groups of pollinators are bees, bumblebees, beetles, butterflies, hummingbirds, and bats or other mammals (Willmer 2011). These floral characteristics include flower morphology (size, shape, color, and marks in the perianth), floral rewards (nectar, pollen, oils, resins, volatile compounds), and floral phenology. In particular, the bat-pollination syndrome is a phenomenon generally restricted to the tropics and subtropics in the Old and New World (Fleming et al. 2009). According to the literature, the most important floral traits associated with bat-pollination are: 1) nocturnal or crepuscular anthesis (e.g., the flowers open at night or in the period of reduced light during the transition between day and night); 2) pale or dullish colors in the petals (mostly white, pale green/yellow,

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or creamy colors); 3) flagelliflory (flowers suspended on long stalks, away from the tree branches); 4) cauliflory (flowers located directly on large branches or tree trunks); 5) tubular or radially symmetrical flowers that act like a “mask” on the bat snout, but also brush-type inflorescences with many smaller flowers that open near simultaneously; 6) musty, “onion”-like flower odors, sometimes with sulphur-compounds; 7) diluted nectar (up to 17% of sugar); and 8) hexose-rich nectar (e.g., low sucrose content, but high levels of glucose and fructose).

These floral traits probably evolved in most plant families as a modification to an already existing pollination syndrome, such as the moth-pollination or even the hummingbird-pollination syndrome (von Helversen 2003). Although some authors have criticized this generalized concept, because most flowering plants appear to be pollinated by more than one “type” of pollinator, it remains true that bat-pollinated species share morphological characteristics in their flowers, which distinguish them from other plants. In fact, the floral characteristics associated with bat-pollination have evolved in at least 67 plant families around the world, including about 360 plant species pollinated by the nectarivorous bat species that occur in the Neotropics, and belong almost exclusively to the Phyllostomid family (Fleming et al. 2009).

Bat-Pollination And Bromeliads: Early Observations

Considering only floral traits, German biologist Fritz Müller (1897) noted that the yellowish flowers of the Brazilian *Vriesea jonghei* (Libon ex K. Koch) E. Morren opened at night, and emitted “an opossum-like scent,” producing copious nectar (Sazima et al. 1995). This anecdotal remark constitutes the first observation of a bromeliad species with the putative bat-pollination syndrome. However, the first formal hypothesis on bat-pollination among bromeliads came from Otto Porsch (1932), an Austrian biologist who suggested that bats might pollinate some species within the genera *Vriesea*, *Thecophyllum* (whose species are now placed in the genera *Guzmania* and *Werauhia*) and *Alcantarea*, based solely on the nocturnal anthesis and the dull colors of their flowers.

Several decades later, Stefan Vogel (1969) made the first confirmed report of bat-pollination in bromeliads from Brazil. Like his predecessors, he used the floral morphology to predict that at least 14 species of *Vriesea* (most of them now classified as members of *Werauhia*) would be pollinated by bats. However, Vogel was also the first to conduct mist-netting near flowering individuals of the endemic *V. morrenii* Wawra, capturing two individuals of the glossophagine bat *Anoura caudifer* Geoffroy with bromeliad pollen on their fur. In this way, Vogel initiated the path to more detailed studies that shed light into one of the most overlooked plant-animal interactions.

After the publication of Vogel’s observations, the studies of bat-pollination in bromeliads during the 70´s and early 80´s were limited. The study of Salas (1973) realized in Costa Rica on *Vriesea ororiensis* (Mez) L.B. Sm. & Pittendr. was the only contribution on bat-pollination in bromeliads for nearly a decade. However, the observation of chiropterophily seems doubtful and should be confirmed as the species has red bracts and thus fits better within the hummingbird-pollination syndrome.

In the mid-1980's, a couple of German scientists, Otto and Dagmar von Helversen, both scholars in bioacoustics and bat ecology, made observations in another Brazilian bromeliad, *Vriesea bituminosa* Wawra, that was visited by the same glossophagine bat species observed earlier by Vogel (Dobat & Peikert-Holle 1985: 236). Considering these observations, the von Helversen's took living plants of *Werauhia gladioliflora* (H. Wendl.) J.R. Grant and *W. rugosa* (Mez & Wercklé) J.R. Grant all the way to Germany, where their floral nectar was used as food for the captive nectarivorous bat species *Glossophaga soricina* Pallas and *Anoura geoffroyi* Gray (Sazima et al. 1989).

Overview Of Current Knowledge

Since then, our knowledge about bat-pollination in bromeliads has continuously grown. Bat-pollinated bromeliads have been studied in five countries: Brazil, Costa Rica, Venezuela, Bolivia, and recently, Mexico. However, most of the studies were carried out in Brazil, especially by the working group of Ivan and Marlies Sazima, and Silvana Buzato. Furthermore, Otto von Helversen contributed to the ecological knowledge in cooperation with Marco Tschapka.

Currently, it is presumed that, like in other plant families, bat-pollination in bromeliads is a derivative pollination syndrome, evolved from the basal hummingbird-pollination syndrome (Benzing 2000; Kessler & Krömer 2000), and is reported mainly from medium to high altitudes (i.e., Bolivian Andes region, ca. 1150-2400 m asl), but evidence also exists for a lowland species (*Werauhia gladioliflora* in Costa Rica, 40-60 m.a.s.l.; Tschapka & von Helversen 2007).

Figure 1. Inflorescence of *Guzmania calothyrsa* Mez. Photo by Thorsten Krömer.

It is interesting to note that many neotropical nectar-feeding bats can be found in countries with a high bromeliad diversity, like Brazil and Bolivia, but most of the documented examples of bat-pollinators belong to only one genus, the tail-less bats of the genus *Anoura*, which are common at medium to high elevations (Koopman 1981). We know that bat pollination in bromeliads, at least in Bolivia, is related to mid-elevations, and common in humid montane forests with high trees (Kessler

Figure 2. Inflorescence of *Puya ferruginea* (Ruiz & Pav.) L.B. Sm. Photo by Thorsten Krömer.

& Krömer 2000), where bats of this genus are abundant.

As mentioned above, the greatest number of documented cases of bat-pollination can be found within *Vriesea* and *Werauhia* (Grant 1995). In fact, *Werauhia*, including about 93 species of which 80 occur in Costa Rica and Panama (Krömer et al. 2007), could be entirely bat-pollinated, and thus, demonstrate the importance of bats as pollinators and selective agents in the evolution of bromeliads. In earlier studies, these species now placed in *Werauhia* were usually treated as belonging to *Vriesea*.

Up to now, bat-pollination in Bromeliaceae is reported or suggested in seven genera and 24 species, within the 58 genera and about 3352 reported bromeliad species (Luther 2012). Thus, only about 0.8% of all bromeliad species have been proposed to be bat-pollinated, with current reports in *Encholirium* (*E. glaziovii*, *E. vogelii*), *Guzmania* (*G. calothyrsa*[Fig. 1], *G. danielii*, *G. killipiana*, *G. morreniana*, *G. retusa*, *G. sphaeroidea*), *Pitcairnia* (*P. brongniartiana*, *P. trianae*), *Puya* (*P. ferruginea* [Fig. 2]), *Tillandsia* (*T. heterophylla*, *T. macropetala*; Fig. 5 and 6), *Vriesea* (*V. bituminosa*, *V. gigantea*, *V. longicaulis*, *V. longiscapa*, *V. morrenii*, *V. platynema*, *V. sazimae*), and *Werauhia* (*W. gladioliflora*, *W. kupperiana*, *W. ororiensis*, *W. rugosa*; Fig. 3) (Krömer 2003; Fleming et al. 2009; Krömer et al. 2012; Christianini et al. 2013; Aguilar-Rodríguez et al. 2014; in press). Nevertheless, all of the more than 90 species of *Werauhia* share characteristics that suggest they might be chiropterophilous, in addition to one species of *Billbergia* (Krömer et al. 2006, Krömer et al. 2008). In this manner, chiropterophily

Figure 3. Flowers of *Werauhia noctiflorens* T. Krömer, Espejo, López-Ferr. & Acebey. Photo by Thorsten Krömer.

Figure 4. A. *Billbergia robert-readii* E. Gross & Rauh in habitat B. Inflorescence of *Billbergia robert-readii*. Photos by Thorsten Krömer.

has been confirmed in two out of eight subfamilies of the bromeliads, although most frequently in Tillandsioideae. If *Billbergia robert-readii* E. Gross & Rauh (Fig. 4) is indeed pollinated by bats, it would constitute the first report within Bromelioideae.

Most of the bat-pollinated bromeliads studied have zygomorphic bisexual flowers. In addition, excluding some *Vriesea* species with reddish petals (Sazima et al. 1995), most of them have pale green, yellow, or whitish petals and, in most cases, the floral bracts form a "dish" that helps to accumulate the relatively large quantities of nectar produced by their flowers. The flowering pattern is similar among species of different genera, being most common to open only one or two flowers per night, during a long period. Furthermore, nectar traits, mainly sugar composition and concentration are within the range of those present in bat-pollinated species in other families, offering diluted nectar and with more glucose and fructose over sucrose (Krömer et al. 2008).


Figure 5. *Tillandsia macropetala* in habitat. Photo by Thorsten Krömer.

Also, most bat-pollinated bromeliads are epiphytes, and thus may be more accessible to a nectarivorous bat with hovering flight. However, *Encholirium* species are exceptional among chiropterophilous bromeliads, because they

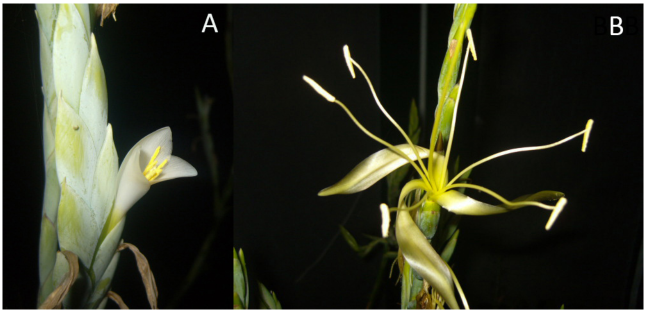

Figure 6. A. Flower of *Tillandsia heterophylla* E. Morren. B. Flower of *Tillandsia macropetala* Wawra. Photos by Pedro Aguilar.

are mainly terrestrial, and with a racemose or brush-like inflorescence bearing many open flowers each night, in contrast to the spike-like inflorescences and epiphytic habit of most other bat-pollinated bromeliads.

The best-documented case of bat-pollination among bromeliads however comes from Costa Rica and the species *Werauhia gladioliflora*. Contrary to other works, this bromeliad has been studied in tropical lowland rainforest of La Selva biological station, where it receives visits by at least four different bat species. It is known that this bromeliad is important to the local nectarivorous bats, providing a valuable resource in the form of nectar and pollen almost all year around (Tschapka & von Helversen 2007).


Figure 8. The nectarivorous bat *Anoura geoffroyi* pollinating a flower of *Tillandsia macropetala*. Photo by Pedro Aguilar.

A Case Study: Bat-Pollination In Mexican Tillandsias

In this final section we will present our ongoing work on a rare case of bat-pollination in *Tillandsia*, the most species-rich genus within the Bromeliaceae. *Tillandsia* comprises about a third of all bromeliads, and most studies report hummingbirds as the main pollinators. However, members of the subgenus *Pseudoalcantarea* have been proposed to be pollinated by nocturnal animals, because of their night-blooming flowers (Benzing 2000).

In a comprehensive study of nectar traits among bromeliads (Krömer et al. 2008), two Mexican species, *Tillandsia macropetala* Wawra (Fig. 6 and 7); which was re-

Figure 9. *Anoura geoffroyi* Gray, the bat-pollinator of *Tillandsia macropetala* and *T. heterophylla* in Veracruz, Mexico. Photo by Pedro Aguilar.

cently recognized as a species distinct from *T. viridiflora* (Beer) Baker (Krömer et al. 2012) and *T. heterophylla* E. Morren (Fig. 3), showed sugar constituents and concentration similar to other bat-pollinated bromeliads, in addition to pale green or white petals and crepuscular blooming. This suggested a probability that those species could be, in fact, bat-pollinated, unlike any other *Tillandsia* species studied before (Gardner 1986).

This hypothesis remained untested until the Master thesis of the first author confirmed that in the endangered humid montane forests of central Veracruz, both species are pollinated by the tail-less nectarivorous bat, *Anoura geoffroyi* (Fig. 8 and 9). This was supported by nocturnal camera recordings, direct captures of bats near inflorescences with fresh flowers, and the presence of bromeliad pollen on the fur of the captured bats (Aguilar-Rodríguez et al. 2014). It is worth noting that in the case of *T. macropetala*, its flowers do not fit the conventional bat-pollination syndrome (Fig. 6B): it has a faint sweet odor (without the sweat/onion-like scent present in *Werauhia*), and an actinomorphic helicoiform corolla, with band-like petals (unlike members of *Vriesea* and *Werauhia*). Whereas *A. geoffroyi* was the only pollinator recorded for *T. macropetala*, the study of *T. heterophylla* interestingly also revealed diurnal pollinators, such as hummingbirds and bees, as its flowers remain open until the next afternoon and their visits produce fruits (Aguilar-Rodríguez et al. *in press*).

This brief overview shows that most of the information on bat-pollination in bromeliads is relatively recent, and still scarce. We hope to continue our work in Mexico, in other locations and with different species of *Tillandsia*, in order to determine the entire range of this previously undescribed interaction. Documenting these plant-pollinator interactions may provide information necessary for the implementation of conservation strategies, and thus we hope to help to secure the survival of both, bromeliads and their bat-pollinators.

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