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Comments/Reflections

Actual folivory in bats: whole leaves as a formerly dismissed trophic item and a potential avenue for self-medication

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Abstract

To date, leaf consumption in bats has not been considered 'true folivory' because bats chew bits of leaves, extract and swallow their juices, and discard their fibre. The term 'leaf fractionation' is used to distinguish this behaviour from true folivory, or the consumption of full leaves, such as exhibited by herbivores. For over three decades, it has been posited that the consumption of entire leaves — leaf fibre included — would require a digestive system incompatible with bats' ability to fly. Natural history observations can amend long-accepted assumptions, however. We observed a common Neotropical frugivorous bat consuming mature leaves in their entirety, without discarding any part. This anecdotal observation begs further investigation, opening the possibility for a shift in our current understanding of bat feeding behaviour. Because the consumption and digestion of whole leaves leave no readily observable trace (i.e., no dropped remains below the roost), this behaviour may be more prevalent than previously appreciated. While feeding exclusively on leaves remains unlikely in bats, our anecdotal observation reveals that true folivory does indeed take place. Our objective in publishing this observation is to invite research on the role of whole leaves in the diets of bats and their physiological implications. Exploring the effect of leaf consumption on potential self-medication is also paramount. Bats, long recognized for their spectacular dietary diversity, may now be known to feed not only on insects, fruit, nectar, pollen, vertebrates, and blood, but also on entire leaves.

Keywords
Chiroptera, diet, herbivory, leaves, self-medication, true folivory.

> "*Although Chiroptera is a very species-rich mammalian order, there are no folivorous bats…*"
>
> Dudley & Vermeij (1992)

1. Introduction

Folivory in bats was first reported almost seventy years ago after finding partially chewed remains of leaves from *Sechium edule* (Chayote) below the roosts of groups of Old World fruit bats (van der Pijl, 1957), and of *Ficus religiosa* (Sacred Fig Tree) below the roost of Neotropical great fruit-eating bats, *Artibeus lituratus* (Greenhall, 1956, 1957). Although Greenhall (1956, 1957) did not speculate as to why leaves were present below the studied roost, van der Pijl (1957) considered the leaf-consumption behaviour to be a disorder, calling it a "a purely dystrophic activity". Later, when reports on bat folivory became more frequent, it gradually became accepted that frugivorous bats occasionally exhibited specific folivorous behaviours: observations consistently described bats chewing bits of leaves, extracting and swallowing their juices, then discarding the fibrous material in the form of oral pellets (Kunz & Ingalls, 1994; Lowry, 1989). All bat folivory reports in Old World fruit bats (i.e., flying foxes) and in Neotropical frugivorous bats consistently describe bats chewing small pieces of leaves (e.g., ca. 6 cm^2; Duque-Márquez et al., 2019), and discarding oral pellets in addition to leaf portions large enough to identify the plants (Table A1 in the Appendix). Even flying foxes that are frequently associated with folivorous habits expel the fibre as oral pellets when chewing leaves (Marshall, 1985; Lowry, 1989), a finding which has also been corroborated experimentally (Nelson et al., 2005).

The reason bats chewed leaves, swallowed only the leaf juices, and always expelled the fibre was unclear, but researchers speculated that by doing so, bats might obtain vitamins and micronutrients not available to them in fruits, proteins essential during pregnancy and lactation but usually scarce in fruits, or secondary metabolites that would act as hormonal precursors that stimulate or inhibit bats' reproductive activity (Kunz & Díaz, 1995). While several studies investigated the chemical profile of some leaves used by bats, it remains unknown whether proteins (Law, 1992; Courts, 1998; Ruby et al.,

2000; Stier & Mildenstein, 2005), minerals (Ruby et al., 2000; Nelson et al., 2005), potential hormonal precursors (Amaro-Luis et al., 2021), or other leaf compounds are indeed used by bats.

In a strict sense, these observations of leaf 'consumption' behaviour in bats were distinguished from 'true folivory', such as that exhibited by herbivores. Etymologically the suffix '-vory' derives from the Latin verb to swallow, and thus 'folivory' implies the actual swallowing of leaves. The term 'leaf fractionation' was deemed more appropriate to describe the behaviour observed in bats because only the liquid portion entered bats' digestive system (Lowry, 1989; Dudley & Vermeij, 1994). Researchers argued that the reason bats exhibited leaf fractionation (i.e., not actual folivory) was because eating whole leaves would be incompatible with the energetic demands of flight (Dudley & Vermeij, 1992; Kunz & Ingalls, 1994). By discarding the indigestible tissue, the bat's digestive tract did not require the anatomical and physiological adaptations found in 'true' folivores (Lowry, 1989; Dudley & Vermeij, 1992; Kunz & Ingalls, 1994). Folivory (sensu stricto) has thus been long considered incompatible with bats because the mass and processing time of leaf tissue would adversely influence the ability to power and sustain flight (Duddley & Vermeij, 1994). For decades, we have accepted that this large group of mammals only 'drink leaf juices' because just the liquid portion of fractionated leaves is swallowed, making bats at best partially folivorous (Kunz & Ingalls, 1994).

Natural history observations of animal behaviour in the wild can be revealing, and can question long-accepted assumptions. We share such a case here. While numerous past studies describe bats chewing and discarding leaf portions, spitting out the pulp and consuming only the liquid, we observed one of the most common Neotropical frugivorous bats, *Carollia perspicillata*, consuming whole leaves. The observation of *C. perspicillata* consuming entire leaves suggests that bats are indeed capable of 'true folivory'. We encourage further research in this area to explore the selection pressures driving this fascinating behaviour.

2. Methods

During a study of bat social behaviour at the Smithsonian Tropical Research Institute in 2020, we observed roosts ($0.8 \times 0.8 \times 2$ m high rectangular concrete structures; roost design from Kelm et al., 2008) placed in the

rainforests adjacent to Soberanía National Park (9°7′42.6″N 79°42′55.2″W), near the town of Gamboa, Panama, with an infrared video camera (Sony HD HDRCX560) and two 60 LED infrared lights. Following the standard recording procedure, the camera was left recording during diurnal periods to follow social interactions, with occasional recordings at night. Recordings started in June 2020 and lasted a year (approximately 292 h and 37 min of roost video recordings). We observed the leaves consumption in one of the night recordings in November 2020. Leaf remains were also found below the roost several times during the study.

3. Results

We observed true folivory behaviour (i.e., the consumption of whole leaves without discarding any part) on the night of November 17, 2020 beginning at 23:17 h. A Seba's short tailed-bat, *Carollia perspicillata* — presumably a male based on previous diurnal observations — entered the roost with two

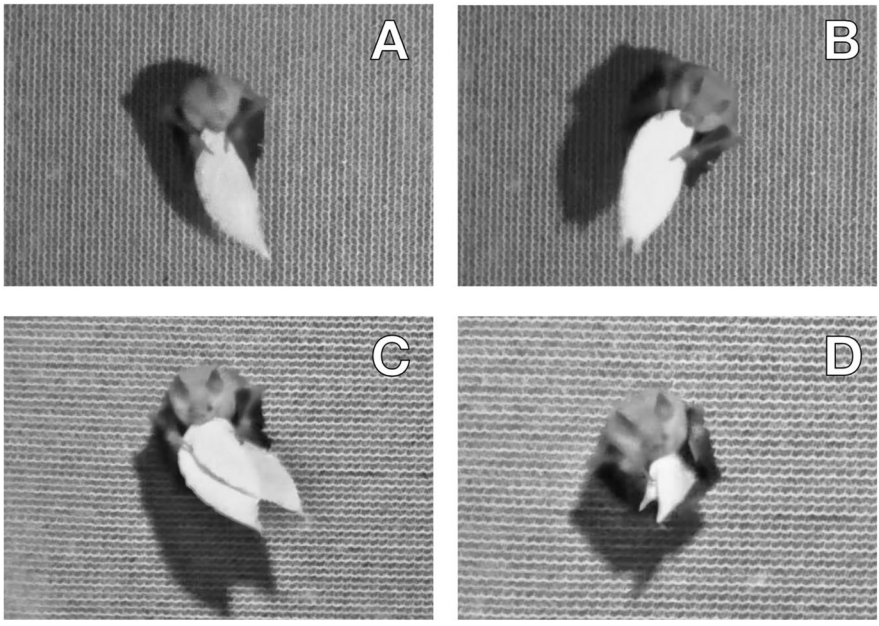

Figure 1. A Seba's short-tailed bat, *Carollia perspicillata*, starting (A–C) and finishing (D) the consumption of two entire leaves inside a roost in forest adjacent to Soberanía National Park, near the town of Gamboa, Panama. For footage of the full 13 min 25 s of this consumption event, see Video 1 at 10.6084/m9.figshare.28052978.

full leaves of an unidentified plant species. This individual started consumption upon arrival in the roost and completed consumption of the two leaves in their entirety by 23:30 h. The consumption of these two full leaves (Figure 1) lasted 13 min 25 s (see Video 1 at 10.6084/m9.figshare.28052978). After consuming the leaves, the bat remained in the roost for three hours, and was observed sleeping, grooming, and excreting several times, before leaving the roost again before dawn.

4. Discussion

This is the first continuous recording of a bat feeding on two leaves without expelling the plant fibre as oral pellets, consistent with the previous intermittent observation of consumption of a single immature leaf (Pereira et al., 2018). Our recording also confirmed the presumed digestion of leaves by uninterruptedly observing the bat for three hours after this ingestion. Leaves were likely mature, as they were fully extended, clearly stiff (i.e., never folded), resembling bay leaves, and produced a crunching sound while being chewed. Moreover, this bat is observed busily chewing each bite in the video, taking a long time to process each bite of both leaves (i.e., tender leaves would be soft and easier to consume). The fact that the bat stayed in the roost for so long (i.e., a quarter of the night) would indicate that it was satiated after consuming these two leaves, both longer than its body length. It was not surprising to observe this individual (likely male) returning to the roost during the night, as harem males usually avoid being away for long periods to protect their roosts and their group of females, and thereby often consume food items within the roost (Kunz & Díaz, 1995). This bat presumably digested the leaves because it remained in the roost for the next three hours, much longer than usual for fruit digestion (approximately 30 min for common frugivores; Morrison, 1980). The first defecation event occurred 28 min after ingestion (00:01:00 h), and nine other defecation events were recorded during the total period of three hours (00:03:20 h; 00:17:22 h; 00:33:18 h; 00:46:11 h; 00:50:20 h; 01:12:05 h; 01:24:30 h; 01:41:38 h; 02:25:57 h). With the exception of a report on *C. perspicillata* in Sergipe, Brazil, in which an individual was observed intermittently for 20 s every minute (i.e., not continuously recorded) presumably consuming a single, tender, and thus less fibrous leaf (Pereira et al., 2018), this is the first observation of its kind, and indicates that bats can indeed consume whole leaves, and could thus be considered exhibiting actual folivorous habits in the true sense of the word. This

is the first time that an uninterrupted recording of a bat consuming mature leaves (note plural) has been shown, in which there is confirmation that the bat does not expel the fibre in the form of oral pellets.

Although bats do not appear to specialize or feed exclusively on leaves, consuming whole leaves may be more common than previous appreciated, and could easily have been overlooked. The consumption and partial or total digestion of whole leaves results in no readily observable evidence. As such, leaf ingestion could go unnoticed if examining faeces through visual inspection, or could be mistaken as fruit consumption, if examining faeces through DNA metabarcoding analysis. Moreover, folivorous habits (both whole leaf consumption, such as we show here, and leaf fractionation) have likely been underestimated as faeces, discarded leaf parts, and oral pellets decompose rapidly, especially in the tropics (Kunz & Díaz, 1995). The mechanisms and routes of absorption of each component present in leaves remain unknown in *C. perspicillata*, and will require extensive research and experimentation. Leaf digestion could require complex biochemical pathways and it remains unclear how frequent this phenomenon is in this and in other bat species. We are just starting to discover and understand the diversity of gut microbiomes (Ingala et al., 2021) and digestion capabilities (Anand & Sripathi, 2004) in bats; it is possible that such processes could allow leaf digestion without the evolution of notable changes in the digestive tract that would counteract or interfere with flight, as was previously believed (Duddley & Vermeij, 1994). While feeding exclusively on leaves remains unlikely in bats due to constraints imposed by flight energetics discussed above (Dudley & Vermeij, 1992; Kunz & Ingalls, 1994), we show that actual folivory in bats does indeed take place, and suggest that it is likely more common than previously thought.

The importance of leaves in the diets of bats is unknown and begs further investigation. For example, although not previously proposed as a formal hypothesis (Kunz & Díaz, 1995), it has been speculated that folivory in bats could play an important role in the control and treatment of infection (Kunz & Ingalls, 1994; Muñoz-Romo & Ramoni-Perazzi, 2020). According to de Roode et al. (2013) traditional examples of animal medication involve animals eating specific plants, as self-medication has been defined as a specific behaviour in which non-human animals self-medicate by selecting and ingesting (or topically applying) plants. For example, it is common to observe diverse animals eating plants to presumably induce vomiting, which

was ruled out in this case as vomiting was not observed for three hours after ingestion. However, a plant could have an effect on the body if ingested without causing vomiting. For example, it is unknown whether defecating ten times would be considered excessive and interpreted as purgation, or it is the expected amount of faeces after feeding on two large leaves. Pharmacological properties of many plant species have been studied as many of them contain bioactive molecules effective in the treatment of various diseases (Riaz et al., 2023). Research is needed to determine whether bats consume leaves as medication when immunocompromised, or whether they use leaves to reduce pathogen infection or decrease ectoparasite loads. Though documented in a wide range of taxa (Clayton & Wolfe, 1993; de Roode et al., 2013; Freymann et al., 2024; Laumer et al., 2024), self-medication has yet to be investigated in bats. Our observation — a frugivorous bat feeding on leaves instead of fruit during a time normally used for active foraging and then spending the next three hours (a quarter of the night) within the roost — suggests that the impact of leaf consumption on bat physiology is far from negligible.

The unambiguous discovery of full leaves consumption recorded in *C. perspicillata* illustrates how fundamental observations of natural history are to our basic understanding of ecology and behaviour. Through this observation, we add a trophic item to bat biology: the consumption of whole leaves, a previously dismissed resource that is abundant, diverse and ubiquitous. This finding invites us to rethink implications of digesting leaves for flying vertebrates. If leaf fractionation behaviour has fascinated biologists for decades, actual folivory in bats is even more striking. Bats, long recognized for their spectacular dietary diversity, can now be known to feed not only on insects, fruit, nectar, pollen, vertebrates and blood, but also on entire leaves.

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Supplementary material

Video 1. Footage of the full 13 min 25 s of leaves consumption by *Carollia perspicillata* in the roost located in the rainforests, near the town of Gamboa, Panama. This video footage can be accessed at 10.6084/m9.figshare.28052978. An additional 3-h video of the bat within the roost, immediately following leaf consumption, is available upon request.

Table A1.
Studies documenting leaf consumption behaviour in bats.

Bat species	Plant species	Actual folivory	Leaf fractionation	References
Neotropical frugivorous species within Phyllostomidae				
Artibeus amplus	*Aspidosperma desmanthum*	No	Yes	Ruiz-Ramoni et al. (2011); Duque-Márquez et al. (2019)
	Brosimum sp.	No	Yes	Ruiz-Ramoni et al. (2011); Duque-Márquez et al. (2019)
	Capparis sp.	No	Yes	Ruiz-Ramoni et al. (2011); Duque-Márquez et al. (2019)
	Clidemia sp.	No	Yes	Ruiz-Ramoni et al. (2011); Duque-Márquez et al. (2019)
	Erythrina sp.	No	Yes	Ruiz-Ramoni et al. (2011); Duque-Márquez et al. (2019)
	Ficus sp.	No	Yes	Ruiz-Ramoni et al. (2011); Duque-Márquez et al. (2019)
	Tapura amazonica	No	Yes	Ruiz-Ramoni et al. (2011); Duque-Márquez et al. (2019)
Artibeus concolor	Unidentified species	No	Yes	Bernard (1997)
Artibeus fimbriatus	*Ficus religiosa*	No	Yes	Esberard et al. (1998)
Artibeus fraterculus	*Colicodendron scabridum*	No	Yes	Arias-Arone & Aguirre-Quispe (2022)
Artibeus jamaicensis	*Calophyllum calaba*	No	Yes	Kunz & Díaz (1995)
	Erythrina poeppigiana	No	Yes	Kunz & Díaz (1995); Rodríguez-Durán & Vásquez (2001)
	Ficus maxima	No	Yes	Silva-Taboada (1979)
	Ficus sp.	No	Yes	Kunz & Díaz (1995)
	Solanum hazenii	No	Yes	Kunz & Díaz (1995)

Table A1.
(Continued.)

Bat species	Plant species	Actual folivory	Leaf fractionation	References
Artibeus lituratus	*Albizia lebbeck*	No	Yes	Novaes & Nobre (2009)
	Erythrina verna	No	Yes	Zortéa & Mendes (1993)
	Eryhrina sp.	No	Yes	Muñoz-Romo & Herrera (2010)
	Ficus religiosa	No	Yes	Greenhall (1956); Greenhall (1957)
	Senna macranthera	No	Yes	Bobrowiec & Cunha (2010)
	Solanum sp.	No	Yes	Muñoz-Romo & Herrera (2010)
	Solanum spp.	No	Yes	Zortéa & Mendes (1993)
	Solanum swartzianum	No	Yes	Zortéa & Mendes (1993)
Artibeus planirostris	*Carica papaya*	No	Yes	Cordero-Schmidt et al. (2016)
	Cynophalla flexuosa	No	Yes	Arias-Arone & Aguirre-Quispe (2022)
	Cynophalla hastata	No	Yes	Cordero-Schmidt et al. (2016)
	Mangifera indica	No	Yes	Cordero-Schmidt et al. (2016)
	Poincianella sp.	No	Yes	Cordero-Schmidt et al. (2016)
	Prosopis juliflora	No	Yes	Cordero-Schmidt et al. (2016)
	Unidentified Euphorbiaceae spp.	No	Yes	Cordero-Schmidt et al. (2016)
	Unidentified Moraceae spp.	No	Yes	Cordero-Schmidt et al. (2016)
	Unidentified species	No	Yes	Cordero-Schmidt et al. (2016)
	Unidentified species	No	Yes	Teixeira et al. (2009)
Carollia perspicillata	*Senna georgica*	Yes*	Yes**	Pereira et al. (2018)
	Unidentified species	Yes*	Yes**	Tthis study

Table A1.
(Continued.)

Bat species	Plant species	Actual folivory	Leaf fractionation	References
Platyrrhinus lineatus	*Solanum lycocarpum*	No	Yes	Aguiar (2005)
	Solanum stipulaceum	No	Yes	Rocha et al. (2016)
	Solanum spp.	No	Yes	Zortéa (1993)
	Unidentified species	No	Yes	Silvestre et al. (2016)
Old World fruit bats within Pteropodidae				
Acerodon jubatus	Unspecified	No	Yes	Stier & Mildenstein (2005)
Cynopterus brachyotis	*Artocarpus fulvicortex*	No	Yes	Tan et al. (1998)
	Cassia fistula	No	Yes	Tan et al. (1998); Rajamani et al. (1999)
	Cassia spectabilis	No	Yes	Tan et al. (1998); Rajamani et al. (1999)
	Erythrina glauca	No	Yes	Tan et al. (1998); Rajamani et al. (1999)
	Erythrina orientalis	No	Yes	Tan et al. (1998); Rajamani et al. (1999)
	Erythrina sp.	No	Yes	Tan et al. (1998)
	Erythrina subumbrans	No	Yes	Tan et al. (1998)
	Erythrina variegata	No	Yes	Tan et al. (1998); Rajamani et al. (1999)
	Eugenia aquea	No	Yes	Tan et al. (1998); Rajamani et al. (1999)
	Eugenia grandis	No	Yes	Tan et al. (1998); Rajamani et al. (1999)
	Eugenia sp.	No	Yes	Tan et al. (1998)

Table A1.
(Continued.)

Bat species	Plant species	Actual folivory	Leaf fractionation	References
	Ficus religiosa	No	Yes	Tan et al. (1998); Rajamani et al. (1999)
	Hevea brasiliensis	No	Yes	Tan et al. (1998); Rajamani et al. (1999)
	Pellacalyx saccardianus	No	Yes	Tan et al. (1998); Rajamani et al. (1999)
Cynopterus sphinx	*Cassia fistula*	No	Yes	Bhat (1994); Rajan et al. (1999); Ruby et al. (2000); Elangovan et al. (2001)
	Cassia siamea	No	Yes	Bhat (1995)
	Coccinia cordifolia	No	Yes	Ruby et al. (2000)
	Coccinia indica	No	Yes	Elangovan et al. (2001)
	Erythrina indica	No	Yes	Bhat (1994)
	Ficus religiosa	No	Yes	Bhat (1994); Ruby et al. (2000); Krishnarathi et al. (2015)
	Holoptelea integrifolia	No	Yes	Bhat (1994)
	Leucaena Ieucocephala	No	Yes	Bhat (1994)
	Mimusops elengi	No	Yes	Elangovan et al. (2001)
	Moringa oleifera	No	Yes	Bhat (1994); Ruby et al. (2000)
	Psidium guajava	No	Yes	Ruby et al. (2000)
	Tamarindus indica	No	Yes	Bhat (1994); Ruby et al. (2000)
Cynopterus spp.	*Ficus* spp.	No	Yes	Marshall (1985)
	Sechium edule	No	Yes	van der Pijl (1957)
	Sechium sp.	No	Yes	Marshall (1985)

Table A1.
(Continued.)

Bat species	Plant species	Actual folivory	Leaf fractionation	References
Eidolon sp.	*Albizia* spp.	No	Yes	Marshall (1985)
	Chlorophora sp.	No	Yes	Marshall (1985)
	Erythrina spp.	No	Yes	Marshall (1985)
	Theobroma sp.	No	Yes	Marshall (1985)
Epomophorus wahlbergi	*Balanites wilsoniana*	No	Yes	Wickler & Seibt (1976); Marshall (1985)
Nyctimene rabori	*Mangifera indica*	No	Yes	Alcazar et al. (2019)
Ptenochirus jagorii	*Aglaia* sp.	No	Yes	Reiter & Tomaschewski (2003)
	Alchornea sp.	No	Yes	Reiter & Tomaschewski (2003)
	Bischofia javanica	No	Yes	Reiter & Tomaschewski (2003)
	Gardenia sp.	No	Yes	Reiter & Tomaschewski (2003)
	Neonauclea calycina	No	Yes	Reiter & Tomaschewski (2003)
	Syzygium xanthophyllum	No	Yes	Reiter & Tomaschewski (2003)
Pteropus alecto	*Albizia lebbeck*	No	Yes	Lowry (1989)
Pteropus dasymallus	*Ardisia sieboldii*	No	Yes	Funakoshi et al. (1993)
	Cinnamomum japonicum	No	Yes	Funakoshi et al. (1993)
	Elaeagnus macrophylla	No	Yes	Funakoshi et al. (1993)
	Elaeocarpus sylvestris	No	Yes	Funakoshi et al. (1993)
	Ficus microcarpa	No	Yes	Funakoshi et al. (1993)
	Ficus superba	No	Yes	Funakoshi et al. (1993)
	Ginkgo biloba	No	Yes	Funakoshi et al. (1993)
	Morus australis	No	Yes	Funakoshi et al. (1993)
	Trichosanthes kirilowii	No	Yes	Funakoshi et al. (1993)

Table A1.
(Continued.)

Bat species	Plant species	Actual folivory	Leaf fractionation	References
Pteropus mariannus	*Artocarpus altilis*	No	Yes	Wiles et al. (1991)
	Guettarda speciosa	No	Yes	Wiles et al. (1991)
	Sonneratia alba	No	Yes	Falanruw (1988)
Pteropus rufus	*Celtis philippensis*	No	Yes	Raheriarisena (2005)
	Tamarindus indica	No	Yes	Raheriarisena (2005)
Pteropus samoensis	*Artocarpus altilis*	No	Yes	Pierson et al. (1996)
	Eria robusta	No	Yes	Pierson et al. (1996)
Pteropus tonganus	*Calophyllum neoebudicum*	No	Yes	Nelson et al. (2005)
Pteropus vampyrus (includes synonym *P. giganteus*)	*Albizia lebbeck*	No	Yes	Aung & Htay (2019)
	Erythrina indica	No	Yes	Krishnarathi et al. (2015)
	Ficus virens	No	Yes	Aung & Htay (2019)
	Tamarindus indica	No	Yes	Aung & Htay (2019)
	Unspecified	No	Yes	Stier & Mildenstein (2005)
Pteropus sp.	*Avicennia* sp.	No	Yes	Marshall (1985)
	Eucalyptus sp.	No	Yes	Marshall (1985)
	Populus sp.	No	Yes	Marshall (1985)
	Sonneratia sp.	No	Yes	Marshall (1985)
Rousettus leschenaultii	*Coccinia grandis*	No	Yes	Krishnarathi et al. (2015)
	Psidium guajava	No	Yes	Krishnarathi et al. (2015)
	Tamarindus indica	No	Yes	Krishnarathi et al. (2015)

Table A1.
(Continued.)

Bat species	Plant species	Actual folivory	Leaf fractionation	References
Rousettus sp.	*Erythrina* sp.	No	Yes	Marshall (1985)
	Ficus sp.	No	Yes	Marshall (1985)

Unidentified species: leaf remains were observed below the roost, but the plant species was not identified.

*Full leaf consumption was inferred from a camera that intermittently recorded (20 seconds every minute) feeding on a single, immature leaf. Whole leaf consumption is highly likely given this video recording, but because the recording was intermittent and not continuous, leaf portion dropping cannot be ruled out.

**Leaf remains were found below the roost during the study, but the species that dropped them has not been confirmed. Unspecified: the bat was observed chewing a leaf and discarding oral pellets.