Phyllomedusa 22(2):195–201, 2023

ISSN 1519-1397 (print) / ISSN 2316-9079 (online)
doi: http://dx.doi.org/10.11606/issn.2316-9079.v22i2p195-201

Short Communication

Notes on facultative use of bat-modified "leaf tents" by *Agalychnis* Red-eyed treefrogs (Anura: Hylidae)

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Keywords: Diurnal retreat, Natural history, Oviposition, Phyllomedusinae, Phyllostomidae.

Palavras-chave: Abrigo diurno, História natural, Ovipostura, Phyllomedusinae, Phyllostomidae.

Oviposition on terrestrial leaves has evolved in multiple lineages of anuran amphibians that portray a wide array of strategies to breed on land (Duellman and Trueb 1986, Wells 2007). In particular, the subfamily Phyllomedusinae (Hylidae; taxonomy following Faivovich *et al*. 2018) is a Neotropical clade that includes typically green treefrogs with vertical pupils commonly known as leaf frogs, which are generally associated to vegetation overhanging lentic environments, where they perch, call, rest, and lay eggs (Duellman 1970, Faivovich *et al*. 2010). Oviposition sites include tree trunks, logs, stems, vines, roots, but more predominantly, leaves (Duellman 1970).

Phyllomedusines show remarkable adaptations that enhance the survivorship of embryos when using leaves as oviposition sites (Pyburn 1970, 1980, Cruz 1990, Warkentin 2000). For instance, parents of *Phyllomedusa* Wagler, 1830 and *Phasmahyla* Cruz, 1991 use their hind limbs to fold leaves around the egg clutches to construct a purse-like, protective ''nest'' composed of one or more curled up leaves that protect egg clutches (Faivovich *et al*. 2010). Alternatively, females of *Cruziohyla* Faivovich, Haddad, Garcia, Frost, Campbell, and Wheeler, 2005 and some *Agalychnis* Cope, 1864 spend some time submerged underwater to fill their bladders before oviposition occurs to subsequently hydrate the egg jelly capsules, which are commonly laid in open leaves (Pyburn 1970).

Duellman (1970) noted that *Agalychnis callidryas* (Cope, 1862) seldom used particular kinds of folded leaves (not constructed by the frogs) to lay eggs but without providing further detail on the plant structures. In the context of these observations, here we report on findings of *Agalychnis* species using bat-modified "leaf tents," which are folded leaf structures constructed by a group of tropical bats of the family Phyllostomidae that modify leaves as shelters (Rodríguez-Herrera *et al*. 2018). Tent production is a relatively poorly documented phenomenon in which bats select leaves of certain plants to build a shelter using their teeth, feet, and thumbs to break or cut some leaf fibers

Received 14 July 2023
Accepted 24 November 2023
Distributed December 2023

(Rodríguez-Herrera *et al*. 2018). The leaves fold down resembling tent-like structures with a variety of architectural designs that offer multiple benefits for bats such as relative permanency, microclimate stability, and reduced risks of predation (Rodríguez-Herrera *et al*. 2008, 2016, Villalobos-Chaves *et al*. 2013). We discuss the implications of this frog-bat interaction with respect to *A. callidryas* and *A. spurrelli* Boulenger, 1913 in terms of diurnal retreats and oviposition sites.

We conducted fieldwork between October 2018 and April 2023 as part of a research project assessing the ecological networks of tent-making bats along the northern edge of the Fila Matama in the Cordillera de Talamanca, Costa Rican Central Caribbean (09°55'21" N, 83°10'2" W, 200–800 m a.s.l.). We conducted more than one hundred days of observations in six years of sampling in an area of approximately 50 km^2, and we registered a total of 130 leaf-tents, which were altogether checked on at least 350 occasions. Field surveys included, but were not exclusive of, the surroundings of artificial breeding ponds used for anuran conservation purposes within the private reserve Veragua Rainforest (see Salazar-Zúñiga *et al*. 2019).

On 08 March 2019 at ca. 08:24 h, we observed an adult *Agalychnis spurrelli* sleeping inside a tent built by *Ectophylla alba* (Allen, 1892) in a *Heliconia trichocarpa* G. S. Daniels and F. G. Stiles leaf at a height of ca. 2 m and located 20 m from the closest pond (Figure 1A–C). On 29 September 2019 at ca. 11:44 h, we observed an adult *Agalychnis callidryas* resting inside of a tent built by *Vampyressa thyone*

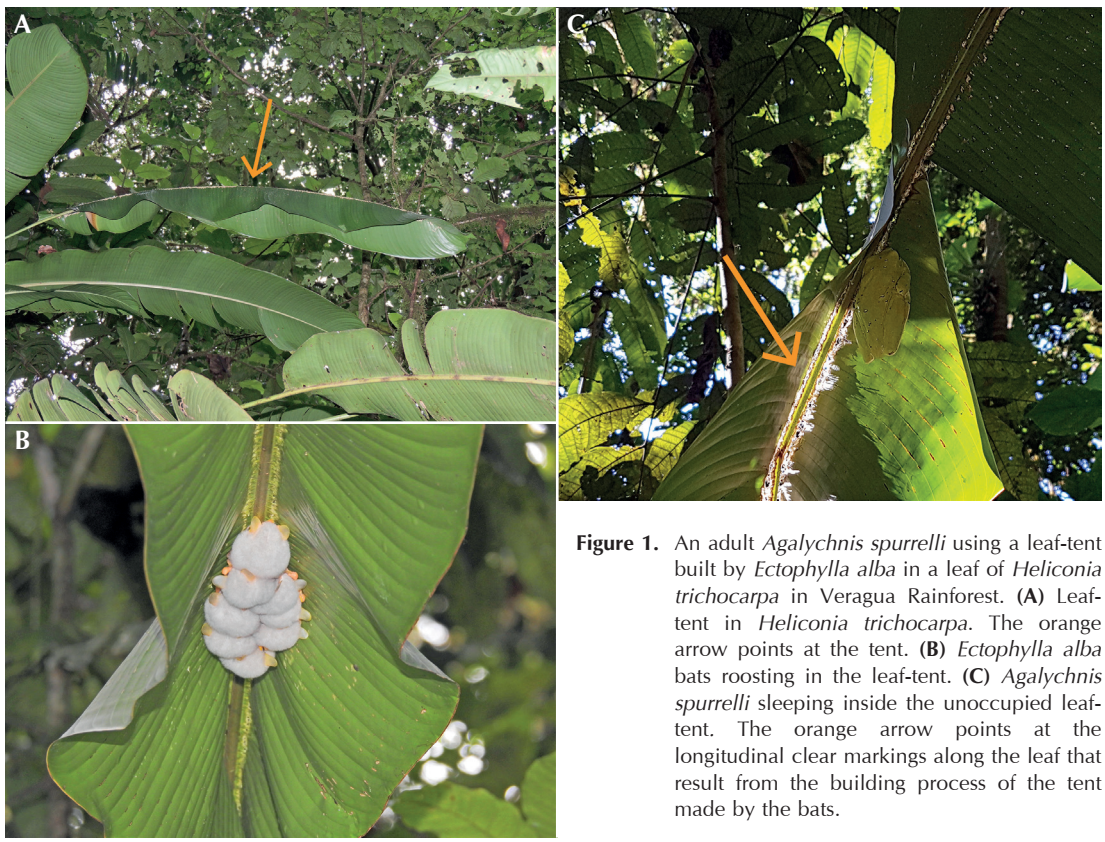

Figure 1. An adult *Agalychnis spurrelli* using a leaf-tent built by *Ectophylla alba* in a leaf of *Heliconia trichocarpa* in Veragua Rainforest. **(A)** Leaf-tent in *Heliconia trichocarpa*. The orange arrow points at the tent. **(B)** *Ectophylla alba* bats roosting in the leaf-tent. **(C)** *Agalychnis spurrelli* sleeping inside the unoccupied leaf-tent. The orange arrow points at the longitudinal clear markings along the leaf that result from the building process of the tent made by the bats.

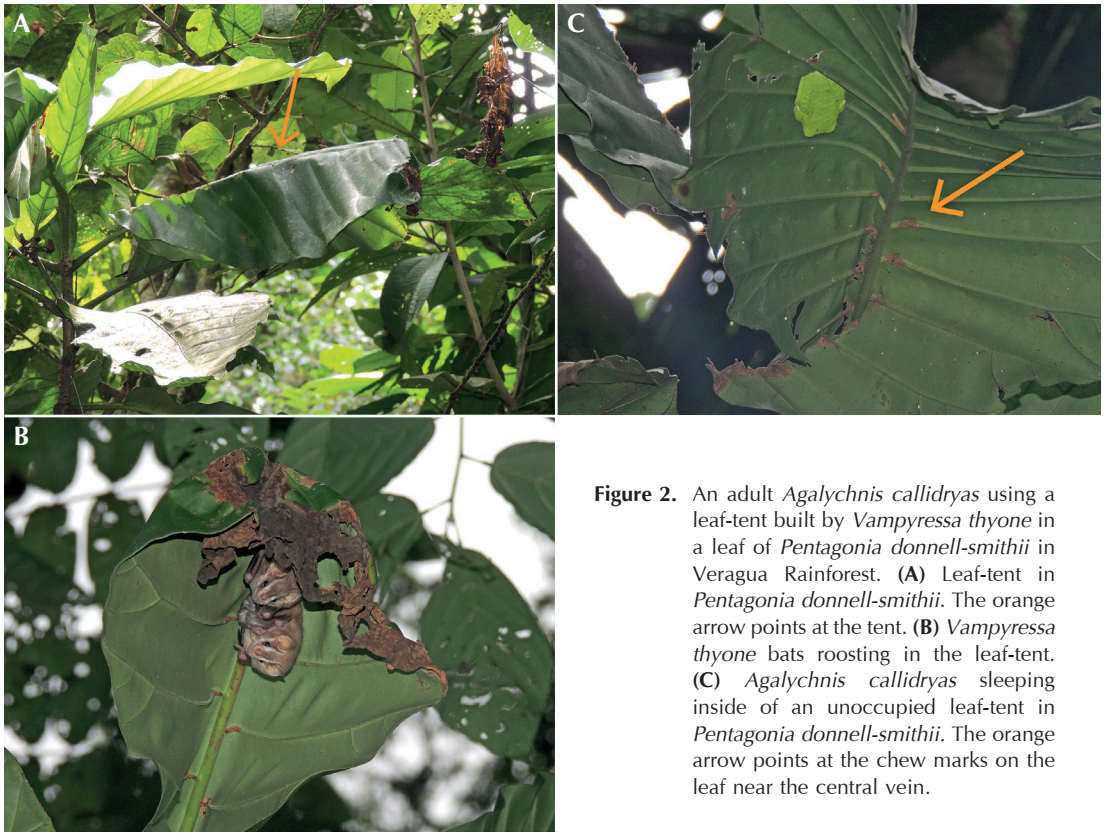

Figure 2. An adult *Agalychnis callidryas* using a leaf-tent built by *Vampyressa thyone* in a leaf of *Pentagonia donnell-smithii* in Veragua Rainforest. **(A)** Leaf-tent in *Pentagonia donnell-smithii*. The orange arrow points at the tent. **(B)** *Vampyressa thyone* bats roosting in the leaf-tent. **(C)** *Agalychnis callidryas* sleeping inside of an unoccupied leaf-tent in *Pentagonia donnell-smithii*. The orange arrow points at the chew marks on the leaf near the central vein.

Thomas, 1909 in a *Pentagonia donnell-smithii* (Standl.) Standl. leaf at a height of ca. 3 m and located ca. 50 m from the closest pond (Figure 2A–C). On 26 February 2020 at ca. 12:04 h, we observed another adult *A. callidryas* resting inside of a second tent built by *E. alba* in a *H. trichocarpa* leaf at a height of ca. 1.5 m and located 30 m from the closest pond. On 15 April 2023 at ca. 09:38 h, we observed an egg clutch of *A. callidryas* in an early developmental stage according to Gosner (1960). The egg clutch was found inside of a third tent built by *E. alba* in a *H. trichocarpa* leaf at a height of ca. 1.5 m, and it was located above a breeding pond (Figure 3A–C). In the eggs of *A. callidryas,* the yolk is pale green in early hatchings and then turns yellowish throughout the development of the eggs, which are evenly distributed within a mass of clear jelly (Duellman 1970; Figure 3B). We monitored the egg clutch on a daily basis as of our initial observation and found it depredated after seven days by an unknown predator (Figure 3C). All tents were unoccupied by bats at the moment of our observations.

Information on interactions between frogs and bats is biased towards predatory events by several bat species (see review in Jacobs and Bastian 2016), with the most notable example being the frog-eating *Trachops cirrhosus* (Spix, 1823), which specializes in echolocating the calls of *Engystomops pustulosus* (Cope, 1864) to prey on calling individuals by eavesdropping on their vocalizations (Tuttle and Ryan 1981). Bats have also been reported as diet items of big-size

Figure 3. An egg clutch of *Agalychnis callidryas* in a leaf-tent built by *Ectophylla alba* in a leaf of a *Heliconia trichocarpa* plant located above an artificial breeding-pond used for anuran conservation purposes. **(A)** Bat-modified leaf-tent. The orange arrow points at the tent. **(B)** Egg clutch inside of an unoccupied leaf-tent. **(C)** Depredated egg clutch.

treefrogs [e.g., *Trachycephalus typhonius* (Linnaeus, 1758) in Strüssmann and Sazima 1991] although these events are seldom documented. Our findings depict a novel interaction between frogs and bats in the form of a potential commensal relationship considering that frogs likely benefit from the shelter built by bats (see below). However, an interesting aspect to consider is the observation that the leaf-tents were unoccupied during our study. This raises the question of whether this can be unequivocally considered a commensal relationship. It is plausible that the bats had abandoned the tents at the point of our observations, challenging the notion of an ongoing commensal association. Both bat species reported in this study are frugivorous and should not represent a predation risk on *Agalychnis* treefrogs. Nonetheless, more research is needed to better interpret the observed bat-frog interactions in this context.

Several frog species have been reported to co-habit with other animals in shelters (not build by the frogs), including burrows (Roznik and Johnson 2009, Simioni *et al*. 2014), termite mounds (Simioni *et al*. 2014), and cracks and crevices in dry soil (Nunes and Costa 2011). However, our findings are the first to document anurans using leaf-made shelters. Leaf tents are usually observed at the understory of the forest and can be functional for several days, weeks or

months (Rodríguez-Herrera *et al*. 2007). Documentation on other organisms taking advantage of bat leaf-tents is scant and restricted to only a handful taxa (e.g., wasps in Timm and Clauson 1990, monkeys in Boinski and Timm 1985). Our observations show that *Agalychnis* species rarely use leaf-tents as we only documented frogs in 1% of our observations and in 3 % of the sampled leaf-tents. However, if available, we presume that bat-modified folded leaves may offer protection to arboreal frogs from adverse environmental conditions during daytime when they retreat (e.g. direct sunlight; see Blaustein and Kiesecker 2002). Although both *Agalychnis callidryas* and *A. spurrelli* spend a considerable amount of time in the canopy of the forest during the day (Duellman 1970), adults may also seek diurnal retreat sites on the understory vegetation after oviposition occurs in the early morning (pers. obs.).

Using bat-tents for oviposition purposes could also preclude the embryos from being detected by certain predators and it could in turn offer appropriate conditions of humidity and temperature on the inside of the tent for the development of the egg clutches (Duellman and Trueb 1986). Yet, this hypothesis remains to be tested pending on a more comprehensive experimental assessment. As shown by our observation, laying eggs inside of already folded leaves does not hinder predation over recently laid clutches. We speculate that the egg mass could have been eaten by a snake given that the entire clutch was consumed (see Warkentin 1995). Frog-eating snakes such as *Leptodeira septentrionalis* (Kennicott, 1859) are commonly observed at the study area eating egg clutches and adults of *A. callidryas* on vegetation above water bodies (see also Pyburn 1963, Wells 2007).

Bat-modified leaf tents may play a more complex role than being only oviposition and resting sites for treefrogs, especially when accounting for the ecology of arboreal anurans that are being protected through the use of artificial ponds for conservation purposes (Salazar-Zúñiga *et al*. 2019). Besides presumably providing frogs and their eggs with a stable environment and keeping them hidden from visual predators, we suspect that since tent-roosting bats are frugivorous, the feces and leftovers of fruits and seeds released during the feeding process could alternatively provide anuran larvae with nutrients in pond-like environments (Gautam *et al*. 2020).

Our speculations regarding the deliberate decision-making process by the frogs in selecting leaf-tents as resting or oviposition sites may indeed be subject to interpretation. It is plausible that the frogs, being arboreal in nature, simply encounter these modified leaf structures incidentally rather than actively seeking them out for specific purposes. Unfortunately, we do not have explicit data on the occurrence of frogs on non-tent leaves, which could provide valuable insights into whether their use of leaf-tents is intentional or coincidental. To better understand the nature of this interaction, we propose that future experiments be conducted, possibly involving the creation of artificial leaf-tents, to assess whether *Agalychnis* frogs actively choose these structures or if their presence is a result of random encounters in their arboreal environment. Controlled experiments could provide valuable insights into the decision-making process of the frogs and help clarify the extent to which this behavior is intentional. While our observations provide a unique insight into a novel interaction between frogs and bat-modified leaf tents, we acknowledge the need for caution in interpreting these behaviors as entirely deliberate. We encourage future studies to assess more deeply the interactions between leaf-tent making bats and treefrogs in the Neotropics.

Acknowledgments.—We thank Bernal Rodríguez-Herrera, Julián Faivovich, Emilia Moreno, and two anonymous reviewers for their helpful comments and thoughts on early discussions regarding the content of this note. WCA thanks ANPCyT (PICT 346/2019), CONICET (PIP2800), and FAPESP (proc. 2021/10639-5).

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Editor: Jaime Bertoluci