



Short communication

Between fruits, flowers and nectar: The extraordinary diet of the frog *Xenohyla truncata*

Carlos Henrique de-Oliveira-Nogueira^{a,*}, Ubiratã Ferreira Souza^{b,c},
Thaynara Mendes Machado^b, Caio Antônio Figueiredo-de-Andrade^d,
Alexander Tamanini Mônico^e, Ivan Sazima^f, Marlies Sazima^g, Luís Felipe Toledo^b

^a Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, Mato Grosso do Sul 79070-900, Brazil

^b Laboratório de História Natural de Anfíbios Brasileiros (LaHNAB), Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, São Paulo 13083-970, Brazil

^c Laboratório de Estudos Herpetológicos e Paleoherpétológicos (LEHP), Departamento de Biologia, Universidade Federal Rural de Pernambuco, Recife, Pernambuco 52171-900, Brazil

^d Instituto de Biodiversidade e Sustentabilidade NUPEM, Universidade Federal do Rio de Janeiro, Macaé, Rio de Janeiro 27965-045, Brazil

^e Programa de Pós-Graduação em Biologia (Ecologia), Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas 69080-971, Brazil

^f Museu de Diversidade Biológica, Universidade Estadual de Campinas, Campinas, São Paulo 13083-863, Brazil

^g Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, São Paulo 13083-862, Brazil

ARTICLE INFO

Keywords:

Animal-plant interactions

Frugivory

Flower-visitation

Pollination

ABSTRACT

Pollination and seed dispersal are determinants for plant survivorship. Among land vertebrates, mammals and birds stand out in these relationships with plants. On the other hand, frogs are not expected to play a role in these interactions, as nearly all species are carnivorous (mostly insectivorous) after metamorphosis. However, one species attracts attention: *Xenohyla truncata*, which includes plant parts on its natural diet. Recently, we observed unexpected interactions between this Neotropical treefrog and plants in their native range. The frog fed on different plant parts, consuming fruits, floral structures and nectar with suction-like movements, and we observed pollen grains adhered to the frog's back, which renders this treefrog as a potential pollinator, besides its already established role as seed disperser. Nectar ingestion during the reproductive season could benefit individuals under high energetic demand. This is a unique and outstanding example of unforeseen interactions between amphibians and plants.

Seed dispersal and pollination play key roles in plant diversity, distribution, and survivorship (Snell et al., 2019; Carvalheiro et al., 2021). Dispersal mechanisms can be physical, such as flight mechanisms and explosive dispersal, or biological, such as animal dispersal (Seale and Nakayama, 2020). Among many forms of dispersal, zoochory (seed-dispersal by animals) and zoophily (pollen transfer by animals), are widespread among endothermic vertebrates (birds and mammals) actively contributing to the dynamics of this diversity (Ollerton, 2017; Snell et al., 2019; Carvalheiro et al., 2021). Ectothermic terrestrial vertebrates (amphibians and reptiles) also are recorded as seed dispersers and floral visitors (Da Silva and Britto-Pereira, 2006; Pietczak et al., 2013; Carvalheiro et al., 2021), but only reptiles play roles as pollinators (Sazima et al., 2005; Ortega-Olivencia et al., 2012; Cozien et al., 2019), even though this relationship is understudied for these

organisms, and no amphibian is recorded as pollinator. It is also worth noting that not all floral visitors qualify as effective pollinators. Some species are larceners that remove the necessary resource from the plant, and cause damage or destruction/consumption of the floral structure (Inouye, 1980; Alves-dos-Santos et al., 2016), not only making its use ineffective through consumption of the resource, but also disabling the structure for animals that would effectively pollinate the flowers.

For post-metamorphic amphibians, consumption of fruit and other plant parts (as leaves and flowers) is known for only a few species (e.g., Isaacs and Hoyos, 2010; Batista et al., 2011; Oliveira et al., 2017; Seveginini et al., 2021; Table 1). Such a diet is suggested to benefit individuals by improving digestion and providing an additional source of water (Anderson et al., 1999). Nevertheless, in these cases the plant ingestion is considered accidental while hunting for invertebrates or

* Corresponding author.

E-mail address: herpeto.nogueira@gmail.com (C.H. de-Oliveira-Nogueira).

<https://doi.org/10.1016/j.fooweb.2023.e00281>

Received 9 January 2023; Received in revised form 22 March 2023; Accepted 23 March 2023

Available online 28 March 2023

2352-2496/© 2023 Elsevier Inc. All rights reserved.

Table 1
Plant species reported in the diet of *Xenohyla truncata* (asterisk indicates alien species).

Plant species	Plant parts	References
<i>Anthurium harrisii</i> (Araceae)	fruit	da Silva et al., 1989; Da Silva and Britto-Pereira, 2006
<i>Cordia taguhyensis</i> (Cordiaceae)	fruit, nectar	This study
<i>Erythroxylum ovalifolium</i> (Erythroxylaceae)	fruit	da Silva et al., 1989; Da Silva and Britto-Pereira, 2006
<i>Iris x germanica</i> (Iridaceae)*	flower	This study
<i>Maytenus obtusifolia</i> (Celastraceae)	fruit	Da Silva and Britto-Pereira, 2006
Not identified	flower	Da Silva and Britto-Pereira, 2006

other animal prey (Anderson et al., 1999; Teixeira et al., 1999; Sabagh and Carvalho-e-Silva, 2008).

Two anuran species, *Euphylyctis hexadactyla* (Asian microglossid) and *Xenohyla truncata* (South American hyliid) are exceptions to the generalized insectivorous/carnivorous diet. For these two frogs, plant parts consumption is intentional, habitual, and probably relevant to their energy intake (Das, 1996; Da Silva and Britto-Pereira, 2006). Between these, the most remarkable case is the one involving the South American treefrog, *X. truncata*, a Vulnerable (VU) to extinction species (Brasil, 2022), Near Threatened (NT) by IUCN, and endemic to the Brazilian Atlantic Forest. This treefrog is restricted to coastal plains (Restinga habitat) of the state of Rio de Janeiro (Frost, 2022), sheltering inside bromeliads and reproducing in temporary ponds (Carvalho-e-Silva et al., 2004). It is omnivorous, with preference for fruits, and preys on invertebrates sporadically (Da Silva and Britto-Pereira, 2006). Thus, this frog is considered as a seed-disperser (da Silva et al., 1989), a unique trait among post-metamorphic amphibians.

During a recent expedition to its natural range in a Restinga environment, we made new records of plant ingestion by *X. truncata*, including the consumption of floral parts (petals and nectar) with suction-like movements, which is a novel information about its feeding habits, and a unique case among amphibians.

We conducted in situ observations of a breeding population of *X. truncata* on 15 December 2020, in a Restinga vegetation area in the municipality of Búzios, state of Rio de Janeiro, southeastern Brazil (22°46'13.94"S, 41°57'4.47" W; WGS84; 2 m a.s.l.), for approximately four hours (from 6:00 to 10:00 pm). Air temperature was 25.8 °C. We observed five individuals of *X. truncata* in feeding activity on two plant species between 7:00 and 9:00 pm. During the observations from a distance of 2 m we used flashlights indirectly pointed toward the focal individuals. Throughout the observation sessions, we used "all sequence" and *ad libitum* sampling methods (Altmann, 1974), which are employed to record temporary or unpredictable events. Pictures (ZUEC-PIC 650) and videos (ZUEC-VID 994–6) of *X. truncata* that resulted from our observations are at the Museu de Diversidade Biológica (MDBio), Universidade Estadual de Campinas, Campinas, São Paulo, Brazil. The research is registered in SISGen (#A3E7CB1) according to Brazil's legislation.

The frogs were feeding on two plant species we found at the Restinga: the native Brazilian milk fruit tree, *Cordia taguhyensis* (Boraginaceae), and the alien bearded iris, *Iris x germanica* (Iridaceae). The former was abundant at the study site, whereas we found only a few individuals of the latter, probably a result of gardening activities at the edge of the Restinga habitat.

At approximately 7:20 pm a *X. truncata* individual (sex undetermined) jumped on a flower of the bearded iris (Fig. 1A), grabbed and bit it starting suction-like movements (Fig. 1B; Video S1). The individual remained on the flower for about 15 min. Afterwards, the frog released what was left of the flower (Fig. 1C) and remained on the plant for about 10 min before jumping toward nearby bromeliads.

Around 8:00 pm we observed other *X. truncata* individuals leaving bromeliads and climbing a Brazilian milk fruit tree full of fruits and flowers. Three individuals (sex undetermined) clustered around a ripe fruit and began a dispute to get close to the fruit, pushing each other away as they tried to bite the fruit (Fig. 1D; Video S2). After approximately five min, two individuals gave in and remained perched on branches close to the fruit, while the third began to nibble the fruit, increasing a pre-existing hole to gain access to the pulp (Fig. 1D). While this individual fed on the fruit, the others no longer disturbed it. The same individual remained nibbling and sucking the fruit pulp for about 10 min, the others eventually approaching to feed.

On the other side of the same tree, we observed a *X. truncata* individual that climbed a branch and entered an open flower (Fig. 1E), where it remained for approximately 5 min performing suction-like movements (Video S3). Upon leaving, pollen grains were adhered to its back (Fig. 1F).

This is the first report of a frog species actively feeding on nectar and flowers in nature and the first evidence that it may act as pollinator. Not only unexpected, but these observations add complexity to the previous reports (da Silva et al., 1989; Da Silva and Britto-Pereira, 2006), suggesting that the interactions of *X. truncata* with plants go beyond fruit feeding and seed dispersal.

Nectar could be highly energetic (Winkler et al., 2009; Araújo and Rocha-Filho, 2019), and sugar concentration in species of *Cordia* spp. may vary from about 14 to 16% (Machado and Loiola, 2000; Dalsgaard, 2011; Wang et al., 2020). At the same time, calling is one of the most physiologically expensive sustained activities performed by an anuran (Taigen and Wells, 1985). Thus, nectar-feeding could be a relevant source of energy for individuals engaged in calling activity and disputes for territory and females. Females also spend a great deal of energy to produce oocytes. Consequently, it could be advantageous to feed on nectar (and fruits) during breeding seasons, as recorded herein.

Not every floral visitor qualifies as a pollinator, as some of them act as cheaters, removing the resources from the plant during feeding and damaging or destroying the flowers (Genini et al., 2010; Alves-dos-Santos et al., 2016), as we observed for *X. truncata* and *Iris x germanica* (Fig. 1B). We suggest that *X. truncata* consumes petals of other flower species as well (see Da Silva and Britto-Pereira, 2006). The opposite happened for *C. taguhyensis*, a native species, where the frog enters the flower and leaves with pollen adhered to skin (Fig. 1E-F).

As mentioned, the relationship between *X. truncata* and the native *C. taguhyensis* is remarkable. The flower structure of *C. taguhyensis* allows *X. truncata* to enter and exit the flower, and to carry pollen grains after the visit. In this case, *X. truncata* could act as a pollinator of this species, or even of other plant species with similar floral structure. However, to play the pollinator role of *C. taguhyensis*, this frog should visit another flower or another plant individual on the same night. We lack information about the breeding system of *C. taguhyensis*, but some *Cordia* species are self-compatible, whereas others are self-incompatible (Opler et al., 1975; Machado and Loiola, 2000; McMullen, 2011; Wang et al., 2020). As *X. truncata* wanders from one plant to another before it settles in a bromeliad for daytime shelter (our pers. obs.), it is likely that the above mentioned scenario about its pollinator role actually occurs.

Species in the genus *Cordia* are visited by a wide variety of invertebrates, such as bees, butterflies, beetles, wasps and flies (Opler et al., 1975; Machado and Loiola, 2000; Lopes et al., 2015), as well as vertebrates such as bats (Alvarez and Quintero, 1970) and birds (Opler et al., 1975; Dalsgaard, 2011; Wang et al., 2020). Thus, *C. taguhyensis* is likely pollinated by multiple animal species and the treefrog *X. truncata* is now a potential pollinator candidate.

Previous information of the consumption of plant parts by *X. truncata* is based on feces and stomach content analyses (da Silva et al., 1989; Da Silva and Britto-Pereira, 2006). Our record is the first observation of this treefrog actively searching and consuming plant parts in nature. Seeds of *C. taguhyensis* are too large to be swallowed by this frog, thus preventing their dispersion as demonstrated or implied for the seeds of

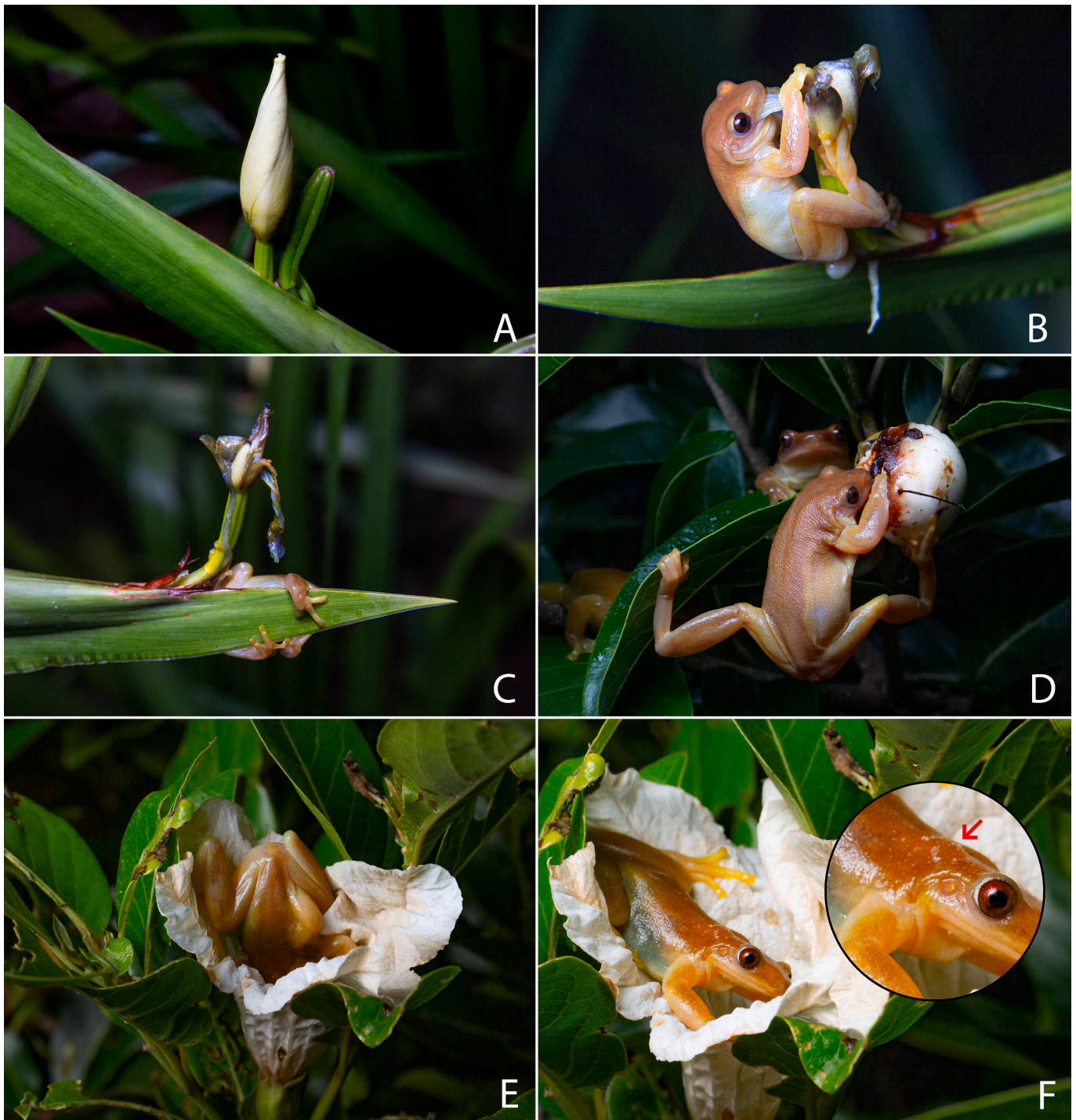


Fig. 1. *Iris x germanica* flower (A). *Xenohyla truncata* eating an *Iris x germanica* flower (B) and its remains after consumption by the frog (C). *X. truncata* nibbling a *Cordia taguhyensis* fruit (D). *X. truncata* within a *Cordia taguhyensis* flower (E), and coming out of it with pollen grains (red arrow) on the back (F). Photographs by C. H. de-Oliveira-Nogueira. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Anthurium harrisii, *Erythroxylum ovalifolium*, and *Maytenus obtusifolia* (da Silva et al., 1989; da Silva and Britto-Pereira, 2006). Da Silva and Britto-Pereira (2006) suggest that color perception may be involved in the *X. truncata* finding and choosing fruits, due the yellow and red colors of the consumed fruits. Likewise, the *C. taguhyensis* fruits are globose, white and conspicuous against the background (Fig. 1). Thus, if colors, or at least contrast is relevant for this treefrog, it could be a model taxon for optical sensitivity studies (e.g., Yovanovich et al., 2017). Anyway, we cannot rule out the possibility of chemical sensing ability to detect these fruits by *X. truncata* as well.

The consumption of fruit species by *X. truncata* seems related to the phenology of the plants in the Restinga habitat (Da Silva and Britto-Pereira, 2006). At the time of our observations, *C. taguhyensis* had many flowers and fruits, and several *X. truncata* individuals were perched on the same plant individual. Our finding strengthens the hypothesis that the consumption of plant parts complement its diet according to fruit availability (Da Silva and Britto-Pereira, 2006). Another use of this type of food would be the accumulation of toxins (Da Silva and Britto-Pereira, 2006), which could protect this treefrog from some predators.

Our observations are not only novel considering an amphibian species' diet, but it is also relevant in providing more natural history information of this threatened to extinction endemic treefrog. The forecast of future climate suitability coupled with sea rise levels have already been suggested as possible causes for the future decline of this species (Oliveira et al., 2016). Now, it is even more important to preserve the populations of *X. truncata*, as its ecological role is unique and distinct from all other living amphibians (Cortés-Gomez et al., 2015). Losing this treefrog species would also imply the extinction of a unique amphibian-plant interaction.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fooweb.2023.e00281>.

Declaration of Competing Interest

We declare that our article is not involved in any interest conflict.

Acknowledgements

We would like to thank the 'Herpeto em Foco' project team for previous discussions and valuable contributions to the first versions of this work. Grants and fellowships were provided by São Paulo Research Foundation (FAPESP #2016/25358-3; #2019/18335-5), the National Council for Scientific and Technological Development (CNPq #142153/2019-2; #302834/2020-6; #300992/79-ZO; #302781/2016-1; #88887.833227/2023-00), and by the Coordination for the Improvement of Higher Education Personnel (CAPES- Finance Code 001).

References

- Altmann, J., 1974. Observational study of behaviour: sampling methods. *Behaviour* 49, 227–267.
- Alvarez, T., Quintero, L.G., 1970. Análisis polínico del contenido gástrico de murciélagos Glossophaginae de México. *An. Esc. Nac. Cienc. Biol. Mexico City* 18, 137–165.
- Alves-dos-Santos, I., Silva, C.I., Pinheiro, M., Kleinert, A.M.P., 2016. When a floral visitor is a pollinator? *Rodriguésia* 67 (2), 295–307. <https://doi.org/10.1590/2175-7860201667202>.
- Anderson, A.M., Haukoos, D.A., Anderson, J.T., 1999. Diet composition of three anurans from the Playa Wetlands of Northwest Texas. *Copeia* 1999, 515–520. <https://doi.org/10.2307/1447502>.
- Araújo, F.P.D., Rocha-Filho, L.C., 2019. Special offer while stocks last: high-energy pulse of nectar caused by a massive post-fire flowering of *Sinningia elatior* (Gesneriaceae) in an area of Cerrado and implications for its pollination. *Rodriguésia* 70, e03462017 <https://doi.org/10.1590/2175-7860201970048>.
- Batista, R.C., De-Carvalho, C.B., Freitas, E.B., Franco, S.C., Batista, C.C., Coelho, W.A., Faria, R.G., 2011. Diet of *Rhinella schneideri* (Werner, 1894) (Anura: Bufonidae) in the Cerrado, Central Brazil. *Herpetol. Notes* 4, 07–21.
- Brasil, 2022. Ministério do Meio Ambiente. Gabinete do Ministro. Portaria MMA N° 148, de 7 de junho de 2022. Diário Oficial da União, 108, p. 74. Available in: <https://www.icmbio.gov.br>.
- Carvalho, L.G., Bartolomeus, I., Rollin, O., Timóteo, S., Tinoco, C.F., 2021. The role of soils on pollination and seed dispersal. *Philos. Trans. R. Soc. B* 376. <https://doi.org/10.1098/rstb.2020.0171>, 2020017120200171.
- Carvalho-e-Silva, S.P., Telles, A.M., Cruz, C.A.G., 2004. *Xenohyla truncata*. The IUCN Red List of Threatened Species 2004 e.T56053A11418199.
- Cortés-Gomez, A.M., Ruiz-Agudelo, C.A., Valencia-Aguilar, A., Ladle, R., 2015. Ecological functions of neotropical amphibians and reptiles: a review. *Univ. Sci.* 20, 229–245. <https://doi.org/10.11144/javeriana.sc20-2.efna>.
- Cozien, R.J., van der Niet, T., Johnson, S.D., Steenhuisen, S.L., 2019. Saurian surprise: lizards pollinate South Africa's enigmatic hidden flower. *Ecology* 100 (3), e01554.
- Da Silva, H.R., Brito-Pereira, M.C., 2006. How much fruit do fruit-eating frogs eat? An investigation on the diet of *Xenohyla truncata* (Lissamphibia: Anura: Hylidae). *J. Zool.* 270, 692–698.
- Da Silva, H.R., Brito-Pereira, M.C., Caramaschi, U., 1989. Frugivory and seed dispersal by *Hyla truncata*, a Neotropical Treefrog. *Copeia* 2, 781–783. <https://doi.org/10.2307/1445517>.
- Dalsgaard, B., 2011. Nectar-feeding and pollination by the Cuban Green Woodpecker (*Xiphidiopicus percussus*) in the West Indies. *Ornitol. Neotrop.* 22, 447–451.
- Das, L., 1996. Folivory and seasonal changes in diet in *Rana hexadactyla* (Anura: Ranidae). *J. Zool.* 238, 785–794. <https://doi.org/10.1111/j.1469-7998.1996.tb05430.x>.
- Frost, D.R., 2022. Amphibian Species of the World: Online Reference. Version 6.1. Available in: <http://research.amnh.org/herpetology/amphibia/index.php>. Accessed on 30 December 2022.
- Genini, J., Morellato, L.P.C., Guimarães, P.R., Olesen, J.M., 2010. Cheaters in mutualism networks. *Biol. Lett.* 6, 494–497. <https://doi.org/10.1098/rsbl.2009.1021>.
- Inouye, D.W., 1980. The terminology of floral larceny. *Ecology* 6, 1251–1253. <https://doi.org/10.2307/1936841>.
- Isaacs, P., Hoyos, J.M., 2010. Diet of the cane toad in different vegetation covers in the productive systems of the Colombian Coffee Region. *S. Am. J. Herpetol.* 5, 45–50. <https://doi.org/10.2994/057.005.0105>.
- Lopes, T.N., Verçosa, F.C., Missagia, C.C.C., 2015. Fenologia reprodutiva e visitantes florais de *Cordia superba* Cham. (Boraginaceae) na vegetação da restinga de Grumari, Rio de Janeiro. *Rev. Biol. Neotrop.* 12, 39–43. <https://doi.org/10.5216/rbn.v11i.30357>.
- Machado, I.C., Loiola, M.I., 2000. Fly pollination and pollinator sharing in two synchronopatric species: *Cordia multispicata* (Boraginaceae) and *Borreria alata* (Rubiaceae). *Rev. Bras. Bot.* 23, 205–311. <https://doi.org/10.1590/S0100-84042000000300006>.
- McMullen, C.K., 2011. Pollination of the heterostylous Galápagos native, *Cordia lutea* (Boraginaceae). *Plant Syst. Evol.* 298, 569–579. <https://doi.org/10.1007/s00606-011-0567-3>.
- Oliveira, S., Roedder, I., Capinha, D., Ahmadzadeh, C., Oliveira, A.F.K.C., Toledo, L.F., 2016. Assessing future habitat availability for coastal lowland anurans in the Brazilian Atlantic rainforest. *Stud. Neotrop.* 51 (1), 45–55. <https://doi.org/10.1080/01650521.2016.1160610>.
- Oliveira, M., Avila, F.R., Tozetti, A.M., 2017. Diet of *Rhinella arenarum* (Anura, Bufonidae) in a coastal habitat in southern Brazil. *Herpetol. Notes* 10, 507–510.
- Ollerton, J., 2017. Pollinator diversity: distribution, ecological function, and conservation. *Annu. Rev. Ecol. Syst.* 48, 353–376. <https://doi.org/10.1146/annurev-ecolsys-110316-022919>.
- Opler, P.A., Baker, H.G., Frankie, G.W., 1975. Reproductive biology of some Costa Rican *Cordia* species (Boraginaceae). *Biotropica* 7, 234–247. <https://doi.org/10.2307/2989736>.
- Ortega-Olivencia, A., Rodríguez-Riano, T., Pérez-Bote, J.L., López, J., Mayo, C., Valtuena, F.J., Navarro-Pérez, M., 2012. Insects, birds and lizards as pollinators of the largest-flowered *Scrophularia* of Europe and Macaronesia. *Ann. Bot.* 109 (1), 153–167. <https://doi.org/10.1093/aob/mcr255>.
- Pietczak, C., Arruda, J.L., Cechin, S.Z., 2013. Frugivory and seed dispersal by *Tropidurus torquatus* (Squamata: Tropiduridae) in southern Brazil. *Herpetol. J.* 23, 75–79.
- Sabagh, L.T., Carvalho-e-Silva, A.M.P.T., 2008. Feeding overlap in two sympatric species of *Rhinella* (Anura: Bufonidae) of the Atlantic Rain Forest. *Rev. Bras. Zool.* 25, 247–253. <https://doi.org/10.1590/S0101-81752008000200013>.
- Sazima, I., Sazima, C., Sazima, M., 2005. Little dragons prefer flowers to maidens: a lizard that laps nectar and pollinates trees. *Biotropica* 5, 1–8. <http://www.biotan.eotopica.org.br/v5n1/pt/abstract?shortcommunication+BN00805012005>.
- Seale, M., Nakayama, N., 2020. From passive to informed: mechanical mechanisms of seed dispersal. *New Phytologist* 225 (2), 653658.
- Severginini, M.R., Moroti, M.T., Pedrozo, M., Ceron, K., Santana, D.J., 2021. Acerola fruit: an unusual food item for the Cururu toad *Rhinella diptycha* (Cope, 1862) (Anura: Bufonidae). *Herpetol. Notes* 13, 7–10.
- Snell, R.S., Beckman, N.G., Fricke, E., et al., 2019. Consequences of intraspecific variation in seed dispersal for plant demography, communities, evolution and global change. *AoB PLANTS* 11, plz016.
- Taigen, T.L., Wells, K.D., 1985. Energetics of vocalization by an anuran amphibian (*Hyla versicolor*). *J. Comp. Physiol. B* 155, 163–170. <https://doi.org/10.1007/BF00685209>.
- Teixeira, R.L., Schineider, J.A.P., Giovanelli, M., 1999. Diet of the toad *Bufo granulosus* (Amphibia, Bufonidae) from sandy coastal plain in southeastern Brazil. *Bol. Mus. Biol. Mello Leitão* 10, 29–31.
- Wang, X., Wen, M., Wu, M., Zhang, D., 2020. *Cordia subcordata* (Boraginaceae), a distylous species on oceanic coral islands, is self-compatible and pollinated by a passerine bird. *Plant Ecol. Evol.* 153, 361–372. <https://doi.org/10.5091/pleveo.2020.1757>.
- Winkler, K., Wäckers, F., Pinto, D.M., 2009. Nectar-providing plants enhance the energetic state of herbivores as well as their parasitoids under field conditions. *Ecol. Entomol.* 34, 221–227. <https://doi.org/10.1111/j.1365-2311.2008.01059.x>.
- Yovanovich, C.A.M., Koskela, S.M., Nevala, N., Kondrashev, S.L., Kelber, A., Donner, K., 2017. The dual rod system of amphibians supports colour discrimination at the absolute visual threshold. *Philos. Trans. R. Soc. B* 372 (1717). <https://doi.org/10.1098/rstb.2016.0066>, 37220160066.