



The Central American Milk Frog, *Trachycephalus “vermiculatus”* (Anura: Hylidae): Observations of Explosive Breeding Activity and a Novel Release Call

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Mesoamerica has a bimodal annual climate, with a dry season typically lasting from January to April and a wet season from June to November. In general, December marks

the beginning of the dry season and May the beginning of the wet season. Many amphibians are prolonged breeders and are active all year round in this tropical realm, although

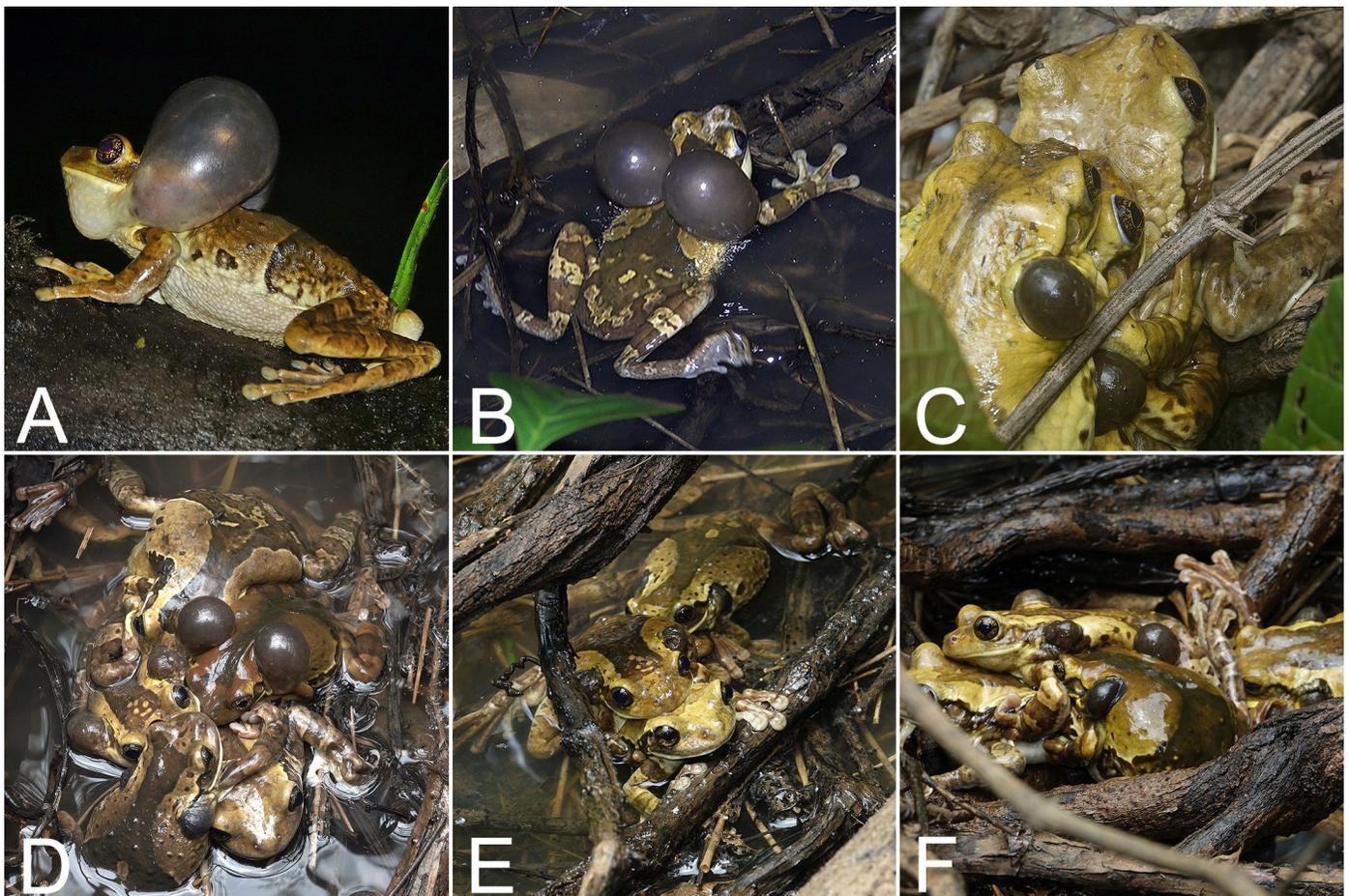


Fig. 1. Central American Milk Frogs (*Trachycephalus “vermiculatus”*) during an explosive reproductive aggregation: Calling male with fully distended vocal sacs (A); calling male floating on water producing small vibrations around the body (B); mating ball consisting of one female with two clasped males (C); mating ball consisting of four males clasped to a single female (D); a satellite male trying to separate a mating pair by positioning its snout between the female and the amplexed male (E); and a fight between several males (F). Photographs by César L. Barrio Amorós.

reproduction for many species is heavily concentrated during the wet season (Duellman 1970; Wells 1977, 2007). Some species of amphibians, many of them in the family Hylidae, are explosive breeders and exhibit a reproductive behavior consisting of large aggregations after the first heavy rains of the wet season. These events can begin in April and May, but also occur throughout the rest of the wet season, according to local rainfall patterns. Explosive breeding is well documented in *Agalychnis spurrelli* (Scott and Starrett 1974; Savage 2002; Thompson et al. 2016; Güell and González 2019; Güell et al. 2019), but it also occurs in the closely related *A. saltator* (Roberts 1994). Several other hylids, including *Scinax boulengeri*, *S. elaeochrous*, *S. staufferi*, *Isthmohyla pseudopuma*, and *Trachycephalus “vermiculatus,”* also are known to concentrate breeding during short periods at the beginning of the wet season (Duellman 1970; Savage 2002). Breeding in these species is different from that of the more abundant hylids, including *Smilisca baudinii*, *Dendropsophus ebraccatus*, and *D. microcephalus*, that reproduce throughout the wet season. Other species belonging to different families, including most microhylids (in Costa Rica *Hypopachus variolosus* and *H. pictiventris*), rhinophrynids (*Rhinophrynus dorsalis*), and bufonids (*Incilius luetkenii*), also are known to breed explosively, especially in dry forest or desertic conditions (Duellman 1970; Savage 2002).

Because Ron et al. (2016) failed to specifically name the milk frogs from Central America and northwestern South America, leaving *Trachycephalus typhonius* for cis-Andean populations (see also Lavilla et al. 2010 for a nomenclatural history), no definitive name applies. In an informal action,

Frost (2022) used the available name *T. “vermiculatus”* (Cope 1877) for the trans-Andean and Mesoamerican populations and we employ that usage herein. This species is widely distributed from Sinaloa, Mexico, southward without a well-defined limit in trans-Andean South America. In Costa Rica this is the only species in the genus and it is widely distributed along the Pacific versant (Savage 2002; Barrio-Amorós 2016; Leenders 2016).

Herein we report observations of explosive breeding in the Central American Milk Frog, *Trachycephalus “vermiculatus.”* We observed the first such event on 18 April 2022 in a small pool beside a dirt road about 80 m from a paved road at Platanillo de Barú, Puntarenas Province, Costa Rica (9.279836°N, 83.821609°W; elev. 235 m asl). The site had an area of about 40 m² around an 8-m² pool that was about 20 cm deep. The surrounding vegetation consisted mainly of dry branches covered in vines and tall grass. The area was a cleared pasture with old cacao plantations and secondary forest. On 17 April a torrential rainstorm started around 1700 h and continued until the following morning around 0600 h. We heard a loud cacophony increasing in intensity throughout the night coming from the small pool. At 1030 h CBA observed the breeding activity at the pool, which could be heard from more than 150 m away. The weather was mostly cloudy with a few short moments of direct sunlight at the pool. The frogs called continuously, but calls were concentrated in choruses every few minutes. We observed two distinct types of calls. The first was an advertisement call used by single males to attract mates (Fig. 1A). Analyses of short audio

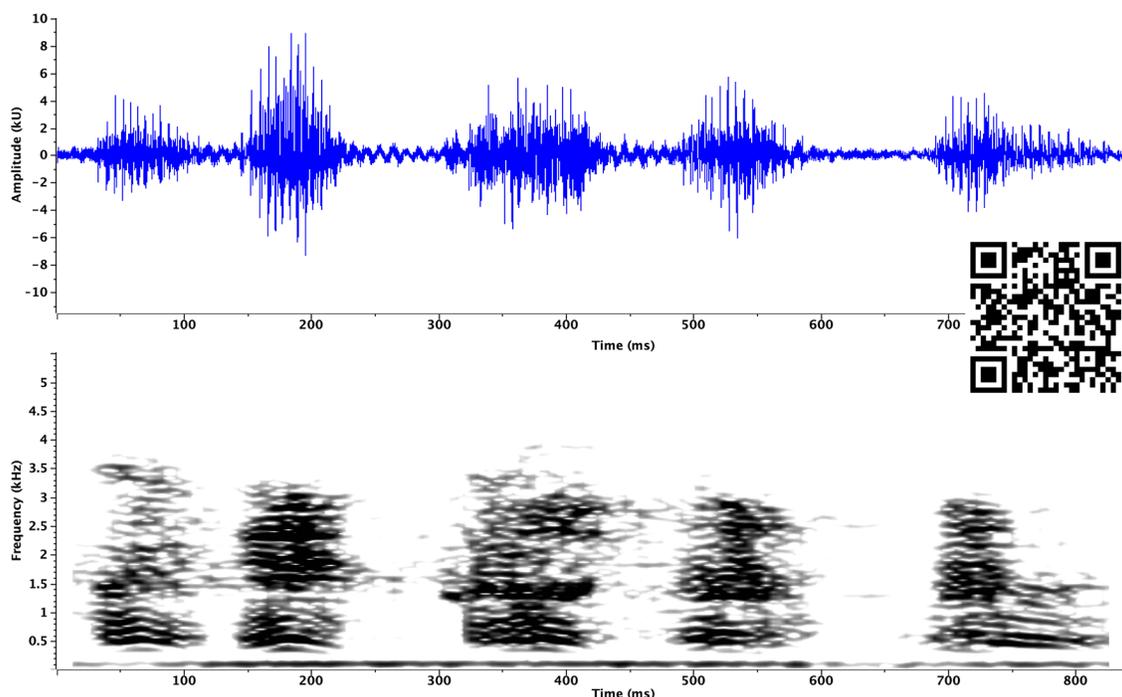


Fig. 2. Waveform and spectrogram of the release call of a male Central American Milk Frog (*Trachycephalus “vermiculatus”*) when clasped by another conspecific male. The embedded QR code links to a video recording in which breeding behavior and calls can be observed.

clips extracted by the Wavepad app for Android showed that the advertisement call of *T. vermiculatus* recorded at our site during these breeding events (26.2 °C) were consistent with those previously documented by Duellman (1970) and Zweifel (1964) and consisted of loud growls 0.23–0.4 s in duration repeated regularly at short intervals with a dominant frequency of 1.39–2.5 kHz.

About 80% of the males called while floating in water, producing small vibrations that were visible around their bodies (Fig. 1B). Other individuals called from low bushes or grass that overhung the water. Many groups of clasped frogs (i.e., mating balls) consisting of one female and two males (Fig. 1C) or of one female surrounded by as many as six males were present (see Fig. 1D for a mating ball consisting of one female and four males); on one occasion, the female was exhausted and showed no signs of mobility but was not dead. Males in these groups fought with each other, pushing other males off the female by introducing their snout between the female and the already amplexed male (Fig. 1E); males also kicked at each other in mating balls (Fig. 1F). Many females in amplexus laid their eggs while elevating their cloacae and expelling small numbers of eggs at a time (Fig. 3A). In the open clear part of the pool, where the activity was most clearly visible, CBA counted as many as eight pairs and six satellite males in an area of about 1 m². We estimated that at the hour of peak activity a total of about 500 *T. vermiculatus* were present in the area. Obviously, animals were not evenly distributed, but our estimates are reasonable, as more activity involving more frogs was evident under the cover of overhanging branches and fewer individuals were active in more exposed parts of the pool. Video and audio recordings for some parts of this breeding event can be viewed via the QR code embedded in Fig. 2.

The second call we observed was a unique release call used by males both during the day and at night when other conspecifics (or males of other species) clasped them in amplexus, either alone or in a mating ball. The release call differed from the advertisement call in that the duration of each note was very short, between 0.06 and 0.09 s, and in that each call had a dominant frequency between 430 and 516 Hz (Fig. 2). Leary and Razafindratsita (1998) described a distinct distress call made by milk frogs in Costa Rica in response to predation; however, we did not observe this call at our site. Interestingly, during advertisement calls the paired vocal sacs of male *T. vermiculatus* were completely inflated, whereas during release calls air sacs inflated only to about half their maximum volume. We deposited the full audio recording in the Colección de Sonidos Ambientales del Instituto Humboldt, Bogotá, Colombia, under the number IAvH-CSA-18835, available at colecciones.humboldt/sonidos upon request to coleccionesbiologicas@humboldt.org.co.

We returned to the site again the next night (18 April 2022) to find several pairs in the pool and its surroundings.

We also observed at least seven interspecific amplexant pairs of male *Agalychnis callidryas* with male or female *T. vermiculatus* (Fig. 3B). We also observed an amplexant pair being stalked by two much smaller male *A. callidryas* (Fig. 3C). The majority of frogs that night were *A. callidryas*, in contrast to the previous night when most individuals were *T. vermiculatus*. Males of both species were calling from vegetation surrounding the area. We observed several dozen amplexant pairs and females laying eggs on every type of substrate, including leaves that were not directly over the water. Hundreds of males were calling and many attempted to clasp anything that moved, including several single male *T. vermiculatus* (Fig. 3B) as well as amplexant pairs (Fig. 3C).

We observed another large breeding aggregation exactly one week later on 25 April 2022. Breeding began around 1830 h after heavy rains earlier that day and a cacophony even more extensive than during the previous event was emanating from the same pond. The water level rose 20 cm and therefore, more than 16 m² of surrounding grass was covered by water. CBA arrived around 1900 h and saw many males arriving at the site from all directions, jumping from the ground and fighting any other male they encountered. We observed no amplexus although several females were present without a mate. The rain intensified and we left the area. Two hours later, it stopped raining and we returned to the pond. At that time, the sound was deafening, many individuals were in amplexus, and many males were fighting. Other single males were calling from branches 1–4 m above the ground and as far as 15 m from the pond. As many as four *Leptodeira* aff. *ornata* were observed, but none were preying on frogs, despite the fact that all of them were surrounded by many individuals. One was coiled with a large distended stomach indicating a recent meal; the prey was likely an *A. callidryas* due to the size of the snake's distended stomach. A large Fer-de-lance ("terciopelo"; *Bothrops asper*) of about 1.3 m was coiled in a prominent place, but seemed uninterested in the frogs (probably aware of their noxious secretions). It fled when disturbed by CBA's presence, ignoring several *Trachycephalus* that easily could have been captured.

At one moment, for some inexplicable reason, all of the *Trachycephalus* stopped calling, and only then were the much less conspicuous calls of the rest of the species present heard clearly. After three minutes, all at once, *Trachycephalus* resumed calling.

We estimated the following proportions of the numbers of individuals of each species: *Trachycephalus vermiculatus* 60%; *Agalychnis callidryas* 15%; *Dendropsophus ebraccatus* 15%; *Scinax elaeochrous* 8%; and *Rhinella horribilis*, *Smilisca phaeota*, *Leptodactylus insularum*, and *L. savagei* 2% each. Our estimates of the numbers of *Trachycephalus* were even greater than during the previous event, with as many as 15 animals per square meter within a much larger (56 m²) pond, likely reaching more than 800 animals.

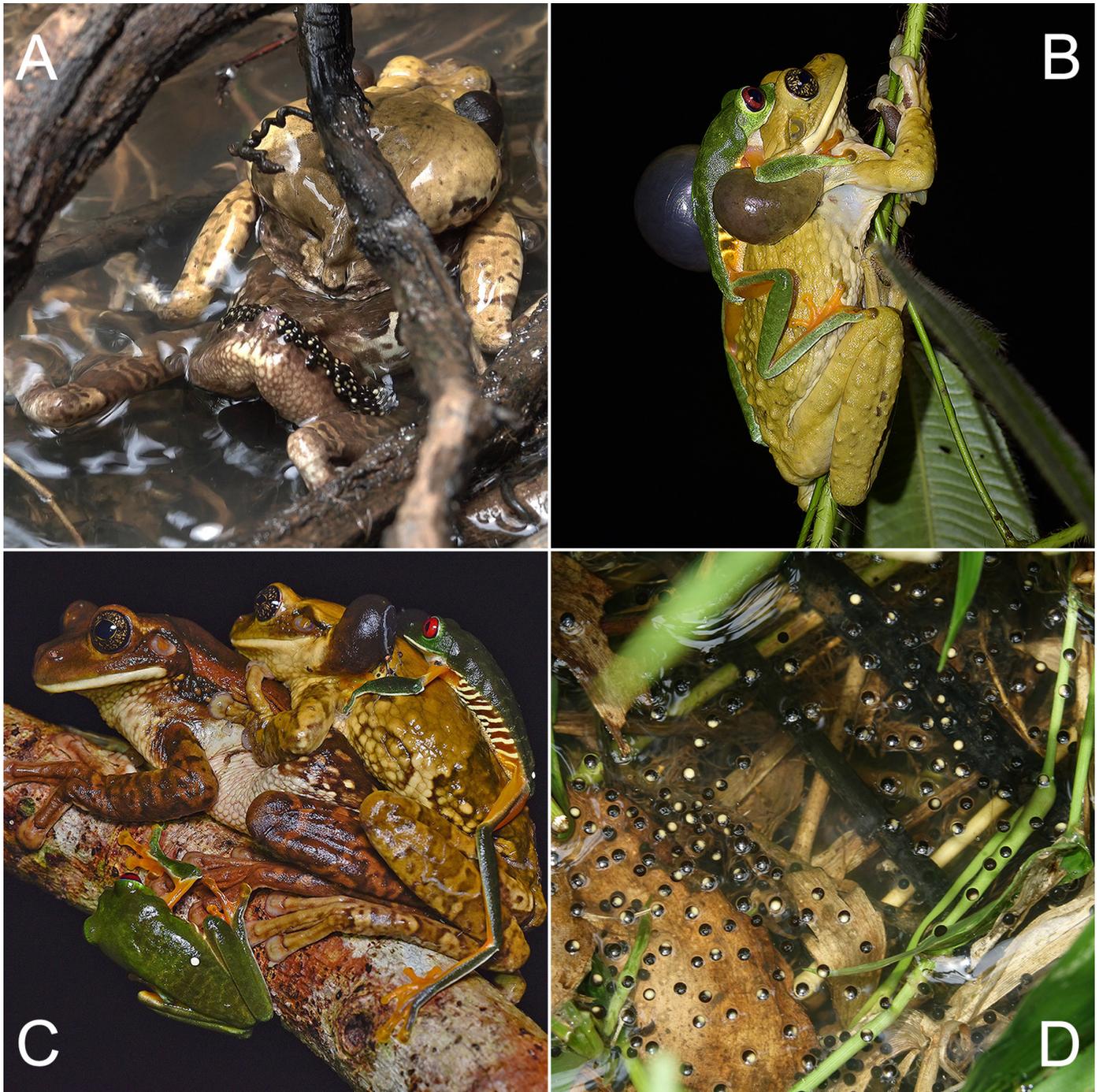


Fig. 3. Central American Milk Frogs (*Trachycephalus* “*vermiculatus*”) during an explosive reproductive aggregation: Female in amplexus elevating its cloaca and expelling eggs (A); a male *T. “vermiculatus*” clasped by a male *Agalychnis callidryas* and emitting a release call (B); an amplexant pair of *T. “vermiculatus*” harassed by two male *A. callidryas* (C); and eggs covered nearly the entire surface of the pond after the last two explosive breeding events (D). Photographs by César L. Barrio Amorós.

That night the rain ceased at about 2300 h, with no more rainfall all night and the next day. The next morning we visited the site at 0745 h. The sun was up and patches of sunlight reached the area. Frog activity was much less conspicuous than during the morning following the first event. Only 12 males were calling actively, with some minutes

between each chorus. *Scinax elaeochrous* was calling as well as a single *Leptodactylus insularum*. We saw few pairs engaged in amplexus but the entire pond was covered with eggs (Fig. 3D). The day was hot and sunny and therefore frogs probably were less active than during cloudier mornings. Males stopped calling around 1100 h.

Acknowledgements

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Literature Cited

- Barrio-Amorós, C.L. 2016. *Amphibians and Reptiles of Costa Ballena, Costa Rica*. Field Museum Field Guides 772: 1–9.
- Duellman, W.E. 1970. The hylid frogs of Middle America. *Monographs of the Museum of Natural History, University of Kansas* 1–2: 1–753. <https://doi.org/10.5962/bhl.title.2835>.
- Frost, D.R. 2022. *Amphibian Species of the World: An Online Reference*. Version 6.1. American Museum of Natural History, New York, New York, USA. <https://doi.org/10.5531/db.vz.0001>. <<https://amphibiansoftheworld.amnh.org/index.php>>.
- Güell, B.A. and K. González. 2019. Mating mayhem. *Frontiers in Ecology and the Environment* 17: 128. <https://doi.org/10.1002/fee.2011>.
- Güell, B.A., K. González, and F. Pedroso-Santos. 2019. Opportunistic predation by two aquatic-feeding predators on an explosive-breeding aggregation of arboreal gliding treefrogs (*Agalychnis spurrelli* Boulenger, 1913; Anura: Phyllomedusidae) on the Osa Peninsula of Costa Rica. *Herpetology Notes* 12: 795–798.
- Lavilla, E.O., J.A. Langone, J.M. Padial, and R.O. De Sá. 2010. The identity of the crackling, luminescent frog of Suriname (*Rana typhonia* Linnaeus, 1758) (Amphibia, Anura). *Zootaxa* 2671: 17–30. <https://doi.org/10.11646/ZOOTAXA.2671.1.2>.
- Leenders, T. 2016. *Amphibians of Costa Rica: A Field Guide*. A Zona Tropical Publication. Cornell University Press, Ithaca, New York, USA.
- Leary, C.J. and V.R. Razafindratsita. 1998. Attempted predation on a hylid frog, *Phrynohyas venulosa*, by an indigo snake, *Drymarchon corais*, and the response of conspecific frogs to distress calls. *Amphibia-Reptilia* 19: 442–446.
- Roberts, W.E. 1994. Explosive breeding aggregations and parachuting in a Neotropical frog, *Agalychnis saltator* (Hylidae). *Journal of Herpetology* 28: 193–199.
- Ron, S.R., P.J. Venegas, H.M. Ortega-Andrade, G. Gagliardi-Urrutia, and P.E. Salerno. 2016. Systematics of *Ecnomiophyla tuberculosa* with the description of a new species and comments on the taxonomy of *Trachycephalus typhonius* (Anura, Hylidae). *ZooKeys* 2016: 115–154. <https://doi.org/10.3897/zookeys.630.9298>.
- Savage, J.M. 2002. *The Amphibians and Reptiles of Costa Rica: A Herpetofauna between Two Continents, between Two Seas*. University of Chicago Press, Chicago, Illinois, USA.
- Scott, N.J. and A. Starrett, A. 1974. An unusual breeding aggregation of frogs, with notes on the ecology of *Agalychnis spurrelli* (Anura: Hylidae). *Bulletin of the Southern California Academy of Sciences* 73: 86–94.
- Thompson, M.E., M.A. Donnelly, and M.S. Mendoza. 2016. *Agalychnis spurrelli* (Gliding Leaf Frog). Explosive breeding aggregation. *Herpetological Review* 46: 434–435.
- Wells, K.D. 1977. The social behaviour of anuran amphibians. *Animal Behaviour* 25: 666–693. [https://doi.org/10.1016/0003-3472\(77\)90118-X](https://doi.org/10.1016/0003-3472(77)90118-X).
- Wells, K.D. 2007. *The Ecology and Behavior of Amphibians*. University of Chicago Press, Chicago, Illinois, USA.
- Zweifel, R.G. 1964. Life history of *Phrynohyas venulosa* (Salientia: Hylidae) in Panama. *Copeia* 1964: 201–208. <https://doi.org/10.2307/1440851>.