Neotropical Biodiversity

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tneo20

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To cite this article: Pol Pintanel , Gabriela Obando-Moreno & Andrés Merino-Viteri (2021) Necrophiliac behaviour in the recently described species Scinax tsachila (Anura: Hylidae), with a review of necrophilia in amphibians, Neotropical Biodiversity, 7:1, 53-56, DOI: 10.1080/23766808.2021.1879549

To link to this article: https://doi.org/10.1080/23766808.2021.1879549

Published online: 01 Feb 2021.

NEOTROPICAL BIODIVERSITY
2021, VOL. 7, NO. 1, 53–56
https://doi.org/10.1080/23766808.2021.1879549

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Necrophiliac behaviour in the recently described species Scinax tsachila (Anura: Hylidae), with a review of necrophilia in amphibians

Pol Pintanel [a,b], Gabriela Obando-Moreno[b] and Andrés Merino-Viteri[b]

[a]Department of Evolutionary Ecology, Estación Biológica de Doñana, CSIC, Sevilla, Spain; [b]Laboratorio de Ecofisiología and Museo de Zoología (QCAZ), Escuela de Ciencias Biológicas, Pontificia Universidad Católica Del Ecuador, Quito, Ecuador

ABSTRACT

Necrophilia in amphibians is a poorly known behaviour despite its potential as a beneficial adaptation for improving reproductive success. Here, we describe the observation of a multiple amplexus involving necrophilia in the recently described Tsachila snouted treefrog, *Scinax tsachila* (Anura: Hylidae). We further provide an extensive review of published necrophilia in amphibians. At least 33 species of amphibians, mostly anurans, have shown a necrophiliac behaviour, with only one case of necrophilia in a caudate. Necrophilia has long been considered a maladaptive behaviour, since reproduction is usually not viable and is also associated with increased risk of death. However, necrophiliac behaviour has recently been proposed as an adaptive behaviour for some species because it may result in viable offspring.

ARTICLE HISTORY
Received 20 May 2020
Accepted 19 January 2021

KEYWORDS
Amplexus; Davian behaviour; necrogamy; reproduction; thanatophilia

Necrophiliac behaviour, also known as Davian behaviour, thanatophilia and necrogamy, is a poorly understood behaviour in reproductive ecology involving sexual interactions between living males and dead females or males [1–4]. Despite the associated energetic and time-consuming costs of this behaviour [5], several observations of amphibians in amplexus with dead conspecifics have been registered (Table 1a). Necrophilia in amphibians is mostly present in "explosive breeders" which have short reproductive events, characterized by a scramble competition mating system [6]. Males congregate at breeding areas in higher numbers than females and call or actively search for females. Competition among males is so high that in some occasions unusual amplexus occurs with dead conspecifics, such as females (Table 1a), other species (Table 1b), egg clutches [7], or even plants or inanimate objects [2,8,9].

Here, we report an observation of a multiple conspecific amplexus consisting of two males and one female of the recently described Tsachila snouted treefrog (*Scinax tsachila* Ron et al. [10]) (Figure 1(a)). Reproduction in this species takes place throughout the day during a few rainy days, forming dense aggregations in open temporary ponds (Pintanel, pers. obs.). The observation took place at the highest elevation point known for the species distribution [10], in a temporary pond located in a cloud forest clearing near Mindo (Figure 1(c)), province of Pichincha, Ecuador (0°02′52″S, 78°47′16″W, WGS84; 1207 m a.s.l.). The observation was made on 5 December 2019, at 2138 h, during an explosive breeding event. This natural temporary pond, with an area of approximately 400 m^2 and a maximum depth of 60 cm, has been monitored for 5 years [see 11, pond labelled as TEMP]. The reproduction of four amphibian species has been documented in this pond: *Boana pellucens* (Werner, 1901), *Dendropsophus carnifex* (Duellman, 1969), *Leptodactylus ventrimaculatus* Boulenger, 1902 and *Scinax tsachila* Ron et al. [10]. On the night of the observation, we encountered three adult *L. ventrimaculatus* individuals, and several adult individuals of *D. carnifex* (>100) and *S. tsachila* (>100). However, *S. tsachila* was certainly more abundant than any other species, with a strongly male-biased sex-ratio (more than 10 males to one female). During the night, two males of *S. tsachila* were found amplexing a dead conspecific gravid female (Figure 1(a,b)). It is likely that the female died during the amplexus, since multiple amplexus may cause the death of females by drowning [12,p.26]. The female seemed dead for several hours. The dead female (snout-vent length, SVL: 34.1 mm) and both males (SVL: 34.2 and 29.6 mm) were collected and deposited in the Museo de Zoología (QCAZ) at the Pontificia Universidad Católica del Ecuador in Quito, Ecuador (female: QCAZA76493, males: QCAZA76494 and QCAZA76495). One of the males was found in an axillary amplexus while the other male was found in a lateral amplexus oriented to the right side of the female. The males remained in amplexus position for more than an hour after capture, until we manually separated them. After the individuals were separated, we observed five eggs attached to the female's ventral skin; however, we could not confirm if they were fertilized or if

CONTACT Pol Pintanel polpintanel@gmail.com

Published online 01 Feb 2021

Table 1. Studies that report (a) intraspecific and (b) interspecific necrophilia in amphibians.

Species	References
(A) *Intraspecific necrophilia*	
Anaxyrus terrestris (Bonnaterre, 1789)	[18]
Anaxyrus woodhousii (Girard, 1854)	[22]
Atelopus wampukrum sp. nov. (*spumarius* complex)	[15,p.59]
Bombina variegata (Linnaeus, 1758)	[20]
Bufo bufo (Linnaeus, 1758)	[23]
Bufo spinosus Daudin, 1803*	[2,16]
Dendropsophus columbianus (Boettger, 1892)*	[24]
Dryophytes versicolor (LeConte, 1825)	[5]
Duttaphrynus melanostictus (Schneider, 1799)	[25]
Epidalea calamita (Laurenti, 1768)	[17]
Incilius nebulifer (Girard, 1854)	[26]
Lithobates sylvaticus (LeConte, 1825)	[27]
Melanophryniscus rubriventris (Vellard, 1947)	[28]
Notophthalmus viridescens (Rafinesque, 1820) **	[13]
Osteopilus septentrionalis (Duméril and Bibron, 1841)	[18]
Physalaemus nattereri (Steindachner, 1863)	[29]
Rana boylii Baird, 1854	[30]
Rana cascadae Slater, 1939	[31]
Rana draytonii Baird and Girard, 1852	[32]
Rana huanrenensis Fei, Ye, and Huang, 1990	[33]
Rana temporaria Linnaeus, 1758	[34]
Rana uenoi Matsui, 2014	[21]
Rhinella icterica (Spix, 1824)	[35]
Rhinella jimi (Stevaux, 2002)	[36]
Rhinella marina (Linnaeus, 1758)	[37,38]
Rhinella proboscidea (Spix, 1824)	[3]
Scinax tsachila Ron et al., 2018	(this study)
Trachycephalus typhonius (Linnaeus, 1758)*	[39]
(B) *Interspecific necrophilia (males)*	
Ascaphus truei Stejneger, 1899	[40]
Bufo spinosus Daudin, 1803*	[2]
Dendropsophus columbianus (Boettger, 1892)*	[41]
Pelophylax lessonae (Camerano, 1882)	[19]
Rana aurora Baird and Girard, 1852	[42]
Rana pretiosa Baird and Girard, 1853	[42]
Tomopterna delalandii (Tschudi, 1838)	[43]
Trachycephalus typhonius (Linnaeus, 1758)*	[44]

* Reported intra- and inter-specific necrophilia for the species
** The only caudate species presenting necrophiliac behaviour

they came out from the female given the reproductive frenzy in the pond during the observation.

We collected information on the necrophiliac behaviour of amphibian species from literature, listed in Table 1. There are at least 33 cases of Davian behaviour in amphibians. All of these cases were in anurans, except for one unusual case in newts, which involved cannibalism and necrophilia simultaneously [13]. Interspecific necrophiliac behaviour has been reported in eight species (Table 1b). Necrophilia is primarily due to two causes: (1) Incorrect recognition of living females by males, as seen in the field and experimentally demonstrated in toads [2,9] or (2) death by drowning during amplexus [12]. For instance, given that multiple amplexus increases the risk of drowning, females of *Rana temporaria* Linnaeus, 1758 feign death to avoid amplexus as males may reject these females. Additionally, females may make male release calls or rotate to try to dissuade males [14]. Also, there is a case of amplexus in an undescribed species of harlequin frog, genus *Atelopus*, in which female's death was likely caused by the fungal pathogen *Batrachochytrium dendrobatidis*, since both individuals were found infected [15,p.59].

Necrophilia has been long considered as a maladaptive behaviour because individuals may lose an opportunity to reproducing successfully [16]. Further, necrophilia may result in an increased predation risk due to longer time spent in the water (breeding sites) [5,17], increased road kills when males engage in amplexus with run over dead females [1,4,18], and may facilitate the propagation

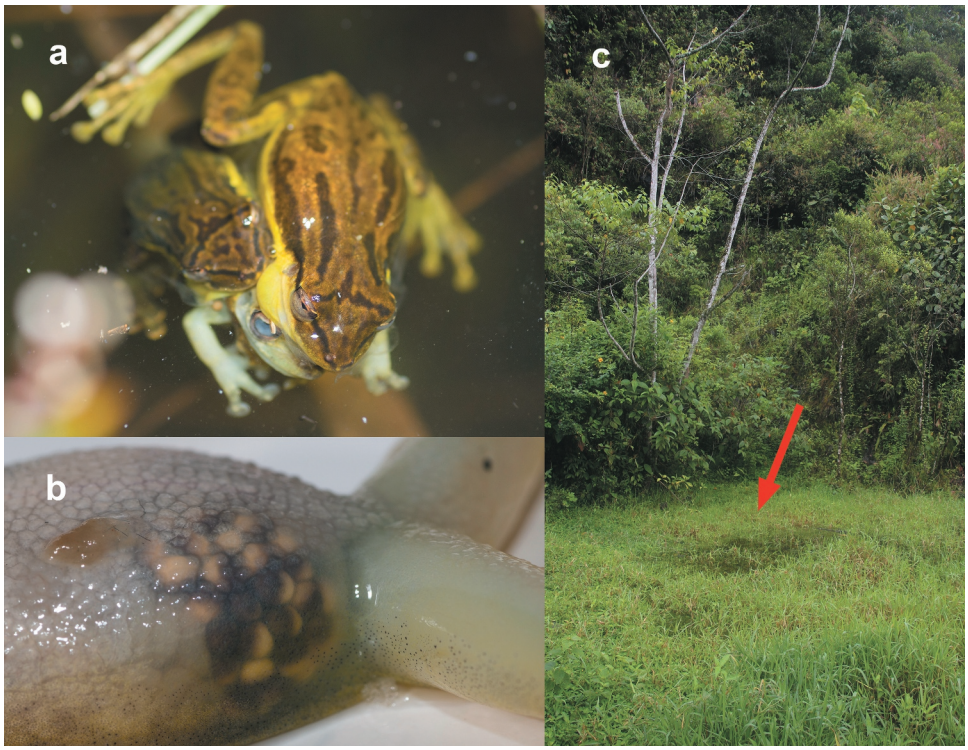

Figure 1. Necrophilia in *Scinax tsachila* from Mindo (Ecuador). (a) Multiple amplexus in *Scinax tsachila* with a dead female, snout-vent length of dead female is 34.1 mm (b) detail of the oocytes through the dead female's skin, (c) site within the open pond (arrow) where necrophiliac behaviour was observed.

of infections [15,19]. However, some authors consider that necrophilia may be functional in some cases. For instance, during explosive breeding events, the cost of amplexing a dead partner may be compensated by the benefit of being the first to encounter a female [20]. In other words, in species with highly biased female-male ratios, engaging in rapid sexual behaviour might be more favourable than being selective. Furthermore, Izzo et al. [3] observed that *Rhinella proboscidea* (Spix, 1824) males can extract and fertilize oocytes from dead females by compressing their abdomen (necrophilia strategy), which has also been proposed for a species of Ranidae [21]. Thus, necrophilia may improve reproductive success in some species of amphibians. However, our observation is not sufficient to prove if necrophilia is indeed a reproductive strategy for *S. tsachila*. Future studies are needed to better understanding the mechanisms and purposes behind this behaviour.

Acknowledgments

We thank Freddy Almeida and Fernando Ayala for helping with fieldwork logistics and Diego Paucar for specimen preparation. We thank Sofia Salinas-Ivanenko and Phil Jervis for helping with the grammar revision, and also PJ for helping with literature. Fieldwork was carried out under permits issued by Ministerio del Ambiente of Ecuador (MAE-DNB-CM-2015-0025-M-0001).

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This study was funded by Dirección General Académica of PUCE through research grant INV0215 IINV529010100.

ORCID

Pol Pintanel http://orcid.org/0000-0002-4256-7377

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