



Cannibalism in the High Andean Titicaca Water Frog, *Telmatobius culeus* Garman, 1875

^{1,*}Arturo Muñoz-Saravia, ²Adriana Aguila-Sainz, ²Ricardo Zurita-Ugarte,
²Gabriel Callapa-Escalera, and ¹Geert P.J. Janssens

¹Laboratory of Animal Nutrition, Ghent University, BELGIUM ²Natural History Museum Alcide d'Orbigny, Cochabamba, BOLIVIA

Abstract.—Cannibalism has been considered as an aberrant behavior, but in amphibians and reptiles, it could play a role in the biology of a population. This paper reports conspecific predation in the Titicaca Water Frog (*Telmatobius culeus*), as the first record of cannibalism of adults in this genus. Heterocannibalism describes cases where adults eat larvae, juveniles, and adults. The phenotypical differences between predator and prey suggest this is a case of cannibalistic polyphenism, where cannibalistic morphs seem to have features that facilitate the predation of the conspecifics. Both females and males were observed to be cannibalistic, and suggestions are proposed regarding why both sexes could benefit from cannibalism, as well as how a high density of a fully aquatic species that shares the habitat, resources, and refuges with other conspecifics increases the chances of encounters and cannibalism.

Keywords. Amphibia, conspecific predation, Critically Endangered, heterocannibalism, anurophagy, size relationships

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Introduction

Intraspecific predation, or cannibalism, is the process of eating an individual of the same species and it is widespread in the animal kingdom (Fox 1975; Polis 1981). It may be important in the population ecology of certain amphibians, where in some genera, such as *Rana* and *Notophthalmus*, conspecifics are reported to consist of 7–25% of all diet items (Polis and Myers 1985). Some of the factors that may stimulate cannibalism include intraspecific predation, environmental and nutritional stress, and high densities, and it may also be part of a reproductive strategy (Fox 1975; Kaplan and Sherman 1980; Polis 1981; Polis and Myers 1985).

In amphibians, as in reptiles, the groups that are more often cannibalized tend to be younger and smaller animals (Polis and Myers 1985). However, in contrast to reptiles, cannibalism among amphibians appears to be important in the biology of these species. Cannibalism may be an important strategy for larvae living in ephemeral habitats, where the pressure on this stage is very high, and the first individuals that will metamorphose and emerge from water are mainly the cannibal morph (Crump 1983). Juveniles are commonly eaten by adult frogs, and this predation of juveniles could be a strategy to remove future competitors for the

predator itself and for its own offspring (Kaplan and Sherman 1980). Juveniles are more often cannibalized before they reach a certain size. Toledo et al. (2007) explain the term of “status inversion,” i.e. the process of turning from prey into predator as anurans increase in body size. Examples of status inversion have been noted in *Conraua*, *Ceratophrys*, some *Leptodactylus*, *Pyxicephalus*, and *Lithobates*, with adults that can prey upon several types of small vertebrates and even conspecifics (Duellman and Trueb 1994). Cannibalism between adult individuals is less frequent and, as explained by Measey et al. (2015), the prey size of a conspecific adult could deliver some negative effects and even the death of the predator. Few reports of conspecific predation of adults are known, with just a couple of examples such as *Ceratophrys* and *Lepidobatrachus llanensis* (Cochran 1955; Hulse 1978; Polis 1981).

Polyphenism is the occurrence of alternative phenotypes in a population that are produced from a single genotype in response to different environmental stimuli (West-Eberhard 1989). The phenomenon of cannibalistic polyphenism and its causes were reviewed by Crump (1983, 1992) and Hoffman and Pfennig (1999), with reference to phenotypic differences in behavior, morphology, growth, or life history between

Correspondence. *arturo.munozsaravia@ugent.be (AMS), nita_513@hotmail.com (AAS), ricardo.onerzline@gmail.com (RZU), ghab.callapa@gmail.com (GCE), geert.janssens@ugent.be (GPJJ)

cannibal and non-cannibal forms and often resulting in expression of the most advantageous phenotype under current environmental conditions (Hoffman and Pfennig 1999). These adaptations include rapid development, larger size, hypertrophied jaw musculature, and more aggressive behavior, among other factors that could facilitate the cannibalism in these morphs.

Lake Titicaca Frog is considered an iconic species, and as one of the largest fully aquatic frogs in the world (Fontúrbel 2009; De La Riva 2005) it has several adaptations to survive in the conditions that a high Andean lake provides. For many years, the taxonomy of the four species of *Telmatobius* described in the Titicaca basin (*Telmatobius albiventris*, *Telmatobius crawfordi*, *Telmatobius culeus*, and *Telmatobius marmoratus*) has been chaotic. In this area, as many as four subspecies of *T. albiventris*, six of *T. culeus*, two of *T. crawfordi*, and four of *T. marmoratus* have been described, bringing the total number of taxa to 16 subspecies belonging to four putative species (De La Riva 2005). As part of the taxonomic revision, Benavides et al. (2002) demonstrated that *T. albiventris*, *T. culeus*, and *T. crawfordi* represent a single taxon, and that *T. culeus* varies noticeably in morphology and body size from *T. marmoratus*. Benavides (2005) suggested the absence of reciprocal monophyly for the two species present in the lake, recognized as *T. culeus sensu lato* and *T. marmoratus*. He also indicated that lacustrine haplotypes are much older than riverine ones, in agreement with the findings of De la Riva et al. (2010) and also as indicated by Aguilar and Valencia (2009). Consequently, *T. culeus* is the only species present in lacustrine habitats.

This report provides the first evidence of cannibalism in Titicaca Water Frog (*Telmatobius culeus*), a Critically Endangered anuran of the High Andes which is fully aquatic and endemic to Lake Titicaca and its surroundings (De La Riva 2005).

Materials and Methods

During November 2008 to December 2015 studies to monitor the species were conducted at different localities on the Bolivian side of Lake Titicaca, Department of La Paz. Monitoring consisted of swimming on the surface of the water with a snorkel, and counting and observing individuals at depths between 0.5 and 7 m. In some cases when an individual was observed, immersions with the snorkel up to 6 m were carried out to capture the frogs. In addition, scuba diving observations were carried out at depths of up to 12 m for longer periods. When individuals were captured, Snout-Vent Length (SVL) and body mass were obtained together with other biotic and abiotic information. Because this species is Critically Endangered, live frogs were not collected. Casually observed individuals were kept for limited time for specific measurements and then returned to the lake.

Results and Discussion

During the study period, three records of wild individuals eating conspecifics were observed, in addition to similar observations of three others in captivity.

- On 20 January 2009 at 1147 h, in the locality of Patapatani, Bolivia (16°4'58.58"S, 69°7'45.47"W) a male individual (Fig. 1a) of *Telmatobius culeus* was captured at a depth of 5.6 m. This individual was maintained alone during one night in an aquarium, and the next day at 0730 h the frog excreted a juvenile of *T. culeus* with the entire body digested except for the bones and some soft tissue.
- The second case occurred in Sicuani, Bolivia (16°5'23.09"S, 69°6'48.50"W) on 4 November 2011. A female individual was captured at a depth of 4 m. After some measurements, it was separated in a container with water for about half an hour. Within that period a sub-adult male individual was vomited up with the head partially digested.
- On 22 January 2013 in Isla de la Luna, Bolivia (16°2'41.24"S, 69°4'8.78"W), a female individual was found dead at 7 m. A post-mortem analysis was carried out and the remains of bones of the legs were found in the intestines of this individual.

This cannibalistic behavior was observed in both wild populations and captive individuals, a fact suggesting that this is a normal behavior in the species. A captive female frog was observed eating two individuals on two different occasions and in another occasion, one male was observed eating a female frog (Fig. 1b,c). Observations also indicate that cannibalism between individuals of different stages is present in the species, with two observations of adult and juvenile frogs eating tadpoles. Cannibalism by larvae was also recorded with two observations of tadpoles attacking and eating other conspecific larvae that were alive, as well as some juveniles that were sick or dead in the same aquarium (Table 1).

Cannibalism in this genus has been recorded so far in *Telmatobius atacamensis* (Barrionuevo 2015), with an adult female preying on a juvenile. Prior to our observations, Pérez (1998) reported the remains of a small anuran in the gut contents of wild *T. culeus*, but the identity of the anuran eaten was not specified. To our knowledge, the present report is the first on conspecific predation of adults in this genus. This behavior could be present in this species, as in *Ceratophrys* and *Lepidobatrachus* (Polis 1981), due to the morphological adaptations and size differences between individuals in the population, making the cannibalism of adult individuals possible. It would be interesting to see if the same behavior happens with other species of the genus where no such size differences exist.

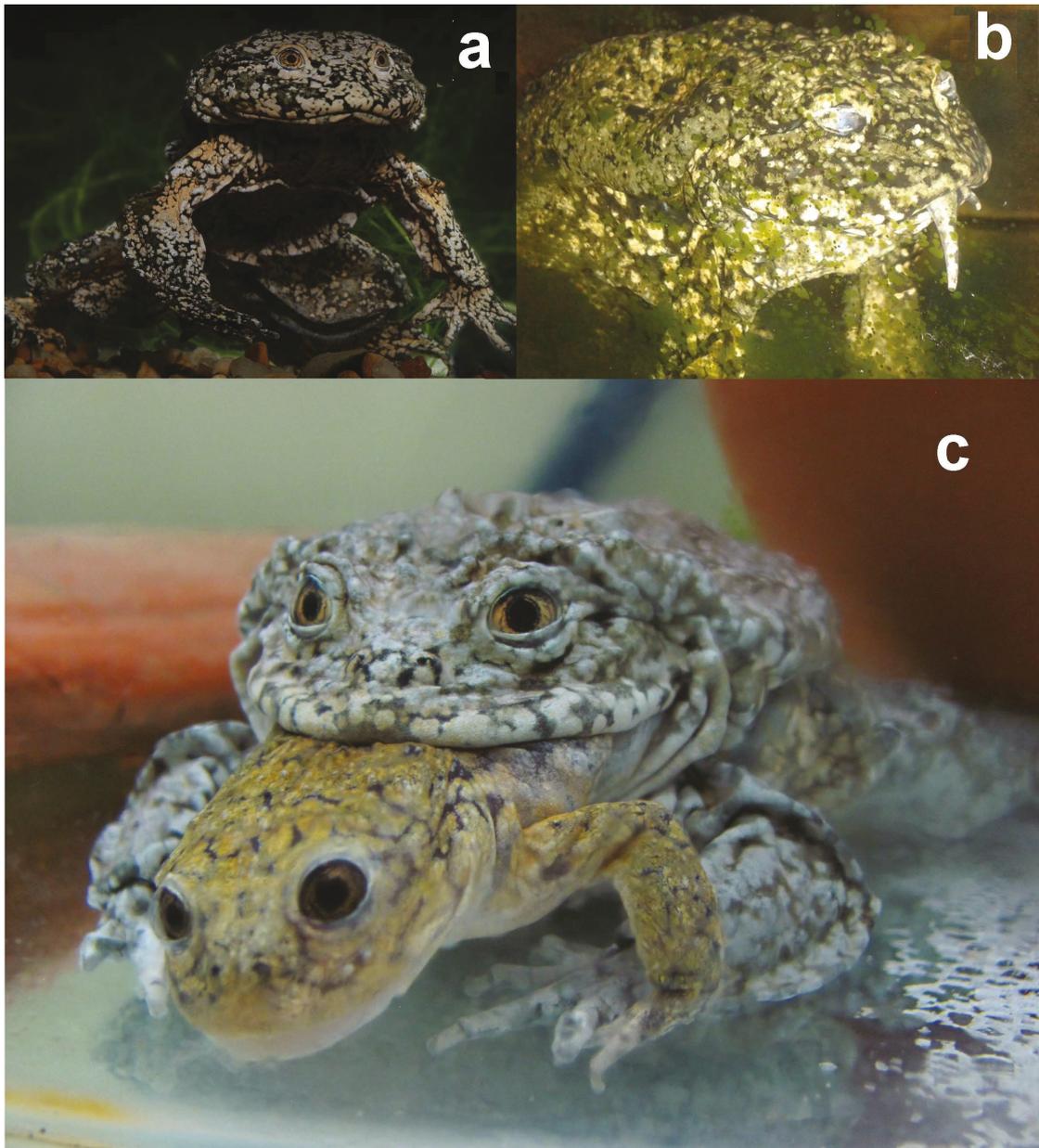


Fig. 1. Individuals of *Telmatobius culeus* eating smaller conspecific frogs: (a) wild male eating a juvenile, (b) female captive frog eating a male adult frog, (c) male captive frog eating a female adult frog. Photos by Arturo Muñoz (a), Patricia Mendoza (b), and Adriana Aguila (c).

Cannibalism may just be opportunistic and occur as a simple by-product of normal predatory behavior (Polis and Myers 1985). Yet, Measey et al. (2015) reported that among 228 anuran species, 77 were known to eat other frogs in different stages. From this last group, cannibalism was identified in 35% of the records. It therefore seems to be a common behavior in anurans, supported by many affirmations (Polis and Myers 1985). The limited number of records of cannibalism in *T. culeus* reported here at least demonstrates that it is present in this species, and in the future more attention should be directed toward seeing if this is a common occurrence in the species. This cannibalistic behavior seems to be associated with taxonomic group, for example taxa such as Ceratophryidae, Hylidae, and Leptodactylidae, all

have elevated levels of anurophagy (Measey et al. 2015). This could be linked with size, where body size is a dominant predictor of anurophagy (Polis 1981; Measey et al. 2015). Since *T. culeus* is considered a large frog (SVL up to 170 mm) and with prominent differences in size between adults, it would make a good candidate for being a cannibalistic species. Adaptations such as a large and wide mouth makes this species prone to predate sizeable prey items, including other anurans and even conspecifics as reported here.

The reasons for cannibalism in a population can be diverse, such as demographic factors where densities are relatively high or where scarce refuge availability increases the chances of encounters (Measey et al. 2015). In some localities, especially in the areas where

Table 1. Details of cannibalism events in wild and captive populations of *Telmatobius culeus*: A = adult, J = juvenile, L = larvae, M = male, F = female, U = undetermined sex.

Locality	Date	Predator characteristics			Prey characteristics		
		Age	Sex	SVL (mm)/weight (g)	Age	Sex	SVL (mm)/weight (g)
Pata Patani	20 January 2009	A	M	112/335	J	U	54/—
Sicuani	4 November 2011	A	F	103/280	A	M	49/—
Isla de La Luna	22 January 2013	A	F	135/302	A	U	N/A
Captive	16 March 2015	A	F	119.4/270	A	M	63.65/28
Captive	16 September 2016	A	F	119.4/270	A	F	62.34/44
Captive	3 January 2017	A	M	91.10/95	A	F	57.18/21
Captive	14 March 2013	A	F	95.6/—	L	U	N/A
Captive	1 May 2013	J	N/A	N/A	L	U	N/A
Captive	4 July 2017	L	N/A	N/A	L	U	N/A
Captive	4 July 2017	L	N/A	N/A	L	U	N/A

cannibalism is reported here, densities of *T. culeus* were relatively high, facilitating the likelihood of individuals finding other frogs that could be eaten. In captive conditions, even with sufficient refuges, cannibalistic events occurred, probably because the chances of encounters were relatively high. Another factor that increases the probability of cannibalism is the similarity of habits that predators and prey share, facilitating their encounters (Measey et al. 2015). In *T. culeus*, as a fully aquatic frog with its entire life cycle under the water, encounters between individuals would be expected to be high and make it easy for large individuals to find tadpoles, juveniles, and even small adults that could be considered as prey.

Heterocannibalism is when there is no genetic relation between a cannibal and its victim (Okuda 2000). There are different reports of its occurrence in aquatic species, such as *Xenopus* and *Pipa*, that are often present in water bodies together with conspecific eggs and tadpoles; and at times when these stages are abundant, they are known to make up a large proportion of the prey eaten (Measey 1998). Here we include two reports of heterocannibalism in captivity in *T. culeus*, but nothing is known about its occurrence in wild populations. Yet, the fact that individuals share the same habitat suggests this kind of cannibalism may also occur in the wild. Similar to *Telmatobius*, *Xenopus* and *Pipa* species lack or have a reduced tongue and rely on suction for most small prey items. They are also able to take large targets through jaw prehension and even the forelimbs are involved in the ingestion of large prey items (Barrionuevo 2016). These are some of the adaptations that *T. culeus*, a fully aquatic species, could use to capture the prey, particularly using the two latter strategies for large prey individuals.

Predating large individuals could be beneficial considering the nutrient intake, but it could also imply costs that result in excessive handling time, as well as a risk of injury to the predator (Wyatt and Forsy 2004). In one of the cases reported here where prey (57.18 mm) and predator (91.1 mm) were of comparable size, the

time that the individual spent trying to ingest the prey was more than 37 hours, involving some costs with the risk of injury during the ingestion and rendering the predatory frog in a vulnerable position against possible predators.

The number of reports on cannibalistic females tends to be higher than for males in the animal kingdom overall (Polis 1981). Despite the low number of observations here, the ratio of four females against two males agrees with that tendency. The great nutritive benefit of such large prey will evidently support the increased nutritional needs of females during the breeding season. Conspecific individuals could thus be a good source of nutrients that makes cannibalism a good option. Even if it is not a common behavior in this species, cannibalism could provide high nutritive value similar to the situation in small fish such as *Orestias*—which are more difficult to catch due to their speed when swimming, when compared with another conspecific prey. Still, males could also benefit from cannibalism, since it allows them to store energy and nutrients for the breeding season. In that regard, it is worth noting that the energy costs for searching and protecting a territory, calling for females, fights, amplexus, and parental care are very high, whereas the males do not eat during this period.

Although cannibalistic polyphenism is known to be present in different species among amphibians (Crump 1983), no information was previously available for *T. culeus*. This species is known to have a great phenotypic variation, to the extent that some have considered there to be different taxa under this name even in the same locality (Benavides et al. 2002). Further studies on this topic would be interesting because all of the cannibalistic frogs reported in this study had the phenotypic features previously ascribed to *Telmatobius albiventris* (now considered *T. culeus*), i.e., all of them were of large size, with wide and big mouths, more robust body and more shaggy skin as seen in Fig. 1. More thorough studies on this topic comparing predator and prey individuals could give us additional information on the likelihood of

cannibalistic polyphenism in this species.

Jiménez and De la Riva (2017) pointed out that cannibalistic lizards predated on large individuals in Andean environments try to optimize digestion by basking to raise their temperature. In the case of *T. culeus*, the species has been reported to bask at hours of higher solar radiation (Muñoz-Saravia et al. 2018), and benefitting digestion could be one of the reasons why these frogs bask. These findings open several questions about the behavior and adaptations of this unique species to some of the extreme conditions found in Titicaca Lake. To determine whether the species really has a cannibalistic behavior or if these are just sporadic observations, could give us more insight about the foraging strategies of the species and the importance of this behavior in the nutrition of the species.

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Arturo Muñoz-Saravia received a Licenciatura in Biology from the state university of Universidad Mayor de San Simón, Cochabamba, Bolivia, and a Ph.D. from Ghent University, Belgium, working on the foraging strategies and nutrition of the Lake Titicaca Frog. Arturo is co-chair of the IUCN SSC Amphibian Specialist Group Bolivia, and has been working with amphibian research and conservation since 1998, focusing on High Andean species.



Adriana Aguila-Sainz graduated in Biology from the state university of Universidad Mayor de San Simón, Cochabamba, Bolivia. She has been working for more than five years in the Natural History Museum Alcide d'Orbigny (Bolivia) in the herpetological department, mainly in the captive breeding component.



Ricardo Zurita-Ugarte graduated in Veterinary Sciences from the state university of Universidad Mayor de San Simón, Cochabamba, Bolivia. He has been working for more than three years in the Natural History Museum Alcide d'Orbigny (Bolivia) in the captive breeding component of the herpetological department.



Gabriel Callapa-Escalera received his Licenciatura in Biology from the state university of Universidad Mayor de San Simón, Cochabamba, Bolivia in 2017. He has worked in the Natural History Museum Alcide d'Orbigny and with Bolivian amphibians for almost ten years on different projects involving research, education, translocations, and conservation in Bolivia. Gabriel is passionate about nature and photography.



Geert P.J. Janssens is a Professor at the Faculty of Veterinary Medicine at Ghent University in Belgium. The research of his team aims to unravel nutrient metabolism in animals across the animal kingdom, often using the principles of comparative nutritional physiology.