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First reproduction of Panha's crocodile newt *Tylototriton panhai* in captivity, with a description of the courtship behaviour, eggs and larval development

AXEL HERNANDEZ[1,2*], PORRAWEE POMCHOTE[3] & ARNAUD JAMIN[4]

[1]Department of Environmental Sciences, Faculty of Sciences and Technics, University Pasquale Paoli of Corsica, Corte, 20250, France
[2]Laboratory for Amphibian Systematic and Evolutionary Research, College of Biology and Environment, Nanjing Forestry University, Nanjing, 210000, China
[3]Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, 10330, Thailand
[4]Le Theil, Le Guedeniau, 49150, France
[*]Corresponding author e-mail: hernandez.axel.1989@gmail.com

ABSTRACT - Amphibians are facing extinction on a global scale and maintaining small populations of threatened or endangered species in captivity is essential. In connection with potential captive breeding of Panha's crocodile newt, *Tylototriton panhai*, we report a detailed husbandry protocol and describe breeding and mating behaviour. After six years in captivity, a group of two adult females and six males, tentatively identified as *T. panhai*, successfully reproduced for the first time on 24th June 2020 after a heavy rainstorm and two subsequent days of precipitation when water temperatures in a large aquaterrarium placed outdoors were 18-21 °C. The complete courtship behaviour consisted of five main stages: i/ approach; ii/ nuptial dance; iii/ amplexus; iv/ spermatophore deposition; v/ fertilisation. The two females laid a total of 84 eggs (41 and 43 eggs each) that were deposited on land in clutches of 4-22 eggs or even singly. Egg size averaged 12.6 ± 0.4 mm and the mean size of the embryo capsule 5.1 ± 0.1 (n=84). The egg hatch success rate was ~80% and on hatching the larvae moved to the water at the bottom of the aquaterrarium. By 7-9 days after hatching the total larval length was 11.89-13.78 mm (n=67). Diagnostic morphological characters are provided for stages 30-46. Metamorphosis occurred at 99-102 days and efts started to move to land at an average total length of 56.2 mm and weight of 0.6-0.9 g.

INTRODUCTION

The newts and salamanders of south-east Asia are amongst the most threatened in the world due to high rates of deforestation, alteration of habitats and human consumption including food and traditional medicine (Hernandez et al., 2019; Pomchote et al., 2020; Bunjerdluk et al., 2021). Thus, the captive maintenance (ex situ) of threatened salamander populations originating from this region is becoming increasingly important (Gagliardo et al., 2008; Browne et al., 2011). However, the husbandry requirements for keeping newts and salamanders in captivity are complex due to their biphasic life cycle, complex ecological needs and reproductive triggers, which may account for why to the present very few conservation programmes have made successful reintroductions into the wild in Southeast Asia (Pasmans et al., 2014; Hernandez, 2016a). For most of the known species, the breeding ecology is still unknown either because most species have only been recently described or because descriptions lack natural history details (Phimmachak et al., 2015; Bernardes et al., 2017). Many species fail to breed under artificial conditions, consequently recording appropriate parameters and protocols that lead to breeding success are crucial for conservation programmes (Hernandez, 2016a,b).

In north-eastern Thailand, several previous attempts have been made to study the biology, distribution and ecology of the poorly known Panha's crocodile newt *T. panhai* Nishikawa, Khonsue, Pomchote & Matsui, 2013 (Hernandez, 2016b,c; Hernandez et al., 2019; Hernandez and Pomchote, 2020; Peerachidacho et al., 2021). Herein, we describe for the first time the breeding success of *T. panhai* in captivity, with a description of courtship, eggs and larval development. *Tylototriton panhai* is a threatened and elusive species with a range that appears to be restricted to the southern parts of Luang Prabang mountain range ecoregion from Phitsanulok, Phetchabun, Uttaradit and Loei provinces, north-eastern Thailand up to Xaignabouli district in Laos at middle elevations between 1,150 m and 1,688 m a.s.l. (Pomchote et al., 2008; Nishikawa et al., 2013; Hernandez, 2016b; Hernandez et al., 2019). The main habitat is composed of *Dipterocapaceae, Lauraceae, Fagaceae*, and *Ericaceae* in evergreen hill forests and montane evergreen broad-leaved forests near various bodies of water (Hernandez and Pomchote, 2020).

Tylototriton panhai is listed as vulnerable (VU) by the IUCN and has been added recently to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) appendix II (IUCN, 2020). Unfortunately, only *Tylototriton verrucosus* is protected by the Wild Animal Protection Act B.E. 2562 (2019) (Department of National

Parks, Wildlife and Plant Conservation, 2021) in Thailand. All known populations of *T. panhai* are small, ecologically restricted and threatened by habitat destruction, pesticide usage, and tourism (Hernandez & Pomchote, 2020; Peerachidacho et al., 2021). The species also shows significant geographic variation as there are three distinct phenotypes isolated on plateaus (Hernandez, 2016b).

MATERIALS & METHODS

Origin and identity of specimens

In July 2012, a group of two females and six males *T. panhai* were purchased from a pet store in Spain that was selling them as *T. verrucosus*. They were acquired for conservation programmes and biological studies at Thoiry Zoological Park (Paris) as previously established for the Critically Endangered Kaiser's mountain newt, *Neurergus kaiseri* (Hernandez, 2016a). The Marcel Bleustein-Blanchet Fund in Paris helped the authors to develop and manage the conservation plan for the genus *Tylototriton* including *T. verrucosus* and its relatives. At the start, animals were housed by the first author during his internship at Thoiry Zoological Park. Then, the specimens were gifted to the first and third authors due to the sale of the conservation area of Thoiry Zoological Park to another administration. Species identification was congruent with the morphological description of *T. panhai* (phenotype II) from northwestern Loei province, Thailand by Hernandez (2016a,b) although their exact geographical origin remains unknown. The eight adult specimens were characterised by wide dorsolateral bony ridges on head, prominent and large rib nodules, spine not quadrate, vertebral ridge distinct and not segmented (Nishikawa et al., 2013). However, morphological identification of crocodile newts is often difficult due to the phenotypic variation known within taxa but *T. panhai* shows distinct characters among *Tylototriton*. All the specimens acquired differed from all other congeners by having widely developed dorsolateral bony ridges on head, black limbs and tail except the edges as previously studied (Nishikawa et al., 2013; Phimmachak et al., 2015). Individuals of *T. panhai* also have very different colour markings that range from orange, yellow to reddish brown on the head, parotoids, lips, the vertebral and dorsal tail ridges, and rib nodules. This colouration is unique among the subgenus *Yaotriton* to which *T. panhai* belongs (Phimmachak et al., 2015). Additionally, the species identity will be confirmed subject to the publication of an analysis of mitochondrial DNA, based particularly on one fragment covering a 930-bp region that encodes part of the NADH dehydrogenase subunit 2 (ND2) and which suggests that the specimens originated from north-eastern Thailand. The sexes were distinguished following Pomchote et al. (2008) and Phimmachak et al. (2015). Adult males showed a pronounced oval to rounded cloaca (Fig. 1A) while females had a conical cloaca especially during the breeding season (Fig. 1B). Moreover, females tend to be robust, larger in size with a distended abdomen and brighter colouration.

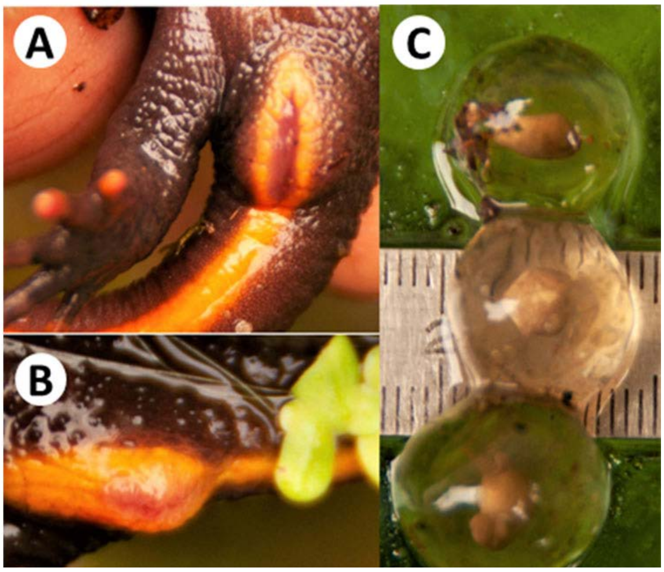

Figure 1. Images of *Tylototriton panhai* - **A**. Cloaca of the male, **B**. Cloaca of the female, **C**. Eggs

Maintenance aquaterrarium

All adult individuals of *T. panhai* were maintained together in a large aquaterrarium (Exo Terra) measuring 120 x 45 x 45 cm (LxWxH) (Fig. 2A). Temperature and humidity were measured with a Bio Dude Digital Thermo/Hygrometer (Houston, Texas), water pH with Expresstech @ LCD PH Medidor Digital (Kingpow Company Limited, China), and other water chemical parameters were taken using drop-by-drop colour tests from JBL (Testlab, Germany). The aquaterrarium was placed in a porch at temperatures between 11-24 °C with a natural circadian rhythm. The substrate was 40 cm deep and 100 cm long in two distinct layers. There was a lower (30-40 cm deep) moist and dark layer composed of clay balls (this substructure ensured good drainage and aeration), loam soil, three large fired-clay bricks, rocks, pieces of cork and other durable bark and an upper dryer layer (10–15 cm deep) consisting of oaks leaves (*Quercus* spp.), mosses (*Kindbergia praelonga*), and plants (*Tradescantia* spp., *Asplenium nidus*). The upperlayer provided a stable humidity of 60-70 % while the lower layer recorded 80-100 %. There was a small permanent pool of water measuring 20 cm long and with a depth of 10 cm. All water used was dechlorinated originating from rainwater at pH 6.6. To increase humidity of the terrestrial substrate, the aquaterrarium was misted with a hand sprayer three times a week. The food source comprised different insects or small invertebrates such as small crickets (*Acheta domestica*), woodlice (*Armadillidium vulgare*) and earthworms (*Dendrobae naveneta*).

From 2012 to June 2020, the crocodile newts showed secretive habits with little crepuscular or nocturnal activity. On 14th July 2019, two male adult specimens showed increased daytime activity and were observed in the pool, they had a lighter appearance; no females were seen. This change in behaviour suggested that a breeding period was imminent and prompted the establishment of an aquaterrarium for breeding as described below.

Breeding aquaterrarium

In June 2020, in an attempt to simulate the natural conditions in which the animals breed during the rainy season, all animals were deposited in a larger aquaterrarium of 200 x 60 x 60 cm furnished with various debris, e.g. rocks, oak leaves and many waterweeds (*Elodea* spp.) (Fig. 2B). This aquaterrarium was placed outdoors for one month. The water depth of the aquatic section was 40 cm with one terrestrial part of 30 x 40 x 30 cm located on the water surface supported by fired-clay bricks, large rocks and bark covered in moss on the upper part for egg deposition. During June 2020, temperatures dropped to 18 °C at night and rose to 24 °C in daytime. Partial water changes of 10-20 %, using cool water, were made every two to three weeks.

Larvae were raised in the same tank as used for breeding except for the addition of a bottom layer of oak leaves in which the larvae could hide. The larvae grew up in stagnant water at temperatures of 18-22 °C. They required feeding once every three days equally spaced with *Daphnia* spp., *Tubifex* spp. and mosquito larvae. After mating and oviposition were complete, all adult specimens were returned to the smaller maintenance aquaterrarium (Fig. 2-A).

All water used in the breeding aquaterrarium was rainwater obtained from empty tanks or water collected from natural springs. No filter was used. Water was acidic to neutral with pH 6.3-7.4, nitrite less than 0.1 ppm, and nitrate less than 10 ppm.

Figure 2. The aquaterraria used for maintenance and then breeding of *T. panhai* - **A**. The aquaterrarium used during the newts' terrestrial phase in September to April placed in a sheltered porch from September to April, **B**. The aquaterrarium used for captive breeding in July/August placed outdoors and with deeper water

RESULTS

Environmental stimuli and preliminary observations of reproductive behaviour

After a hard rainstorm with high air pressure and two subsequent days of precipitation, on a wet day (17th June 2020) two adult males were observed to be more active and showed colourful orange to reddish dorsolateral glandular warts, dorsal ridge, tips of fingers and toes and cloacal parts. They entered the water of the breeding aquaterrarium several times, becoming totally aquatic after two consecutive days at air temperature of 18-20 °C and water temperature 18° C. The four other males followed the first specimens, also becoming partially to totally aquatic between 19th and 21st June 2020. The two females were found to be less active during the first two days in their new aquaterrarium. However, on 20th and 21st June 2020, one or both females were observed entering the water for periods of just a few minutes to 120 minutes during the night time between 21:30-23:00 h. On June 20th and 21st 2020, two males were observed swimming to approach one female during the night. Inter-male competition was observed under water, in which one male attempted to stop the other male from moving in front of the female. Then, the competitor male was engaged in a nudging ritual with one female into the deeper water.

Courtship behaviour

The reproductive behaviour was observed twice and consisted of five main stages as follows:

i) **The approach**

Upon encountering the female, one male was observed presenting its full lateral view of the body to the female. This tentative approach was repeated several times because the female was trying to escape.

ii) **The nuptial dance**

When the female stopped in front of the male, the latter repeatedly circled the female very slowly in front of its head, first sniffing the snout and parotoids region and then, the tail, cloaca, flanks and legs. Both were continuing to sniff each other in a circular manner and turned around several times for about 15-30 minutes.

iii) **Amplexus**

After that, the female pushed the male with its right hindlimb and went under the male (Fig. 3A). The male was seen lying upside down over the female in a submissive manner for few seconds but this attempt failed and was repeated several times (15 minutes to 1 hour), before the male managed to grab the female's forelimbs firmly in its own forelimbs, forming a ventral amplexus position (Fig. 3B).

iv) **Spermatophore deposition**

The male then deposited a cone-shaped spermatophore on the water substrate.

v) **Fertilisation**

Fertilisation was achieved when the spermatophore was taken up into the cloaca of the female.

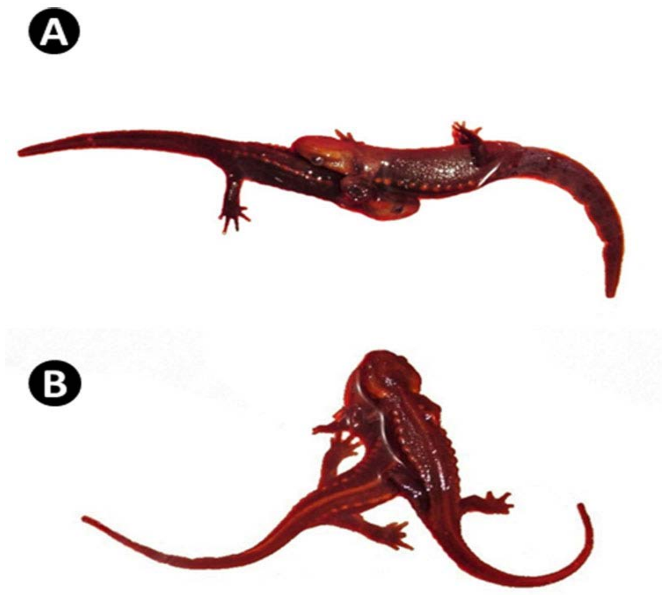

Figure 3. Courtship behaviour of *T. panhai* - **A.** Pre-amplexus of the species, **B.** Ventral amplexus stage

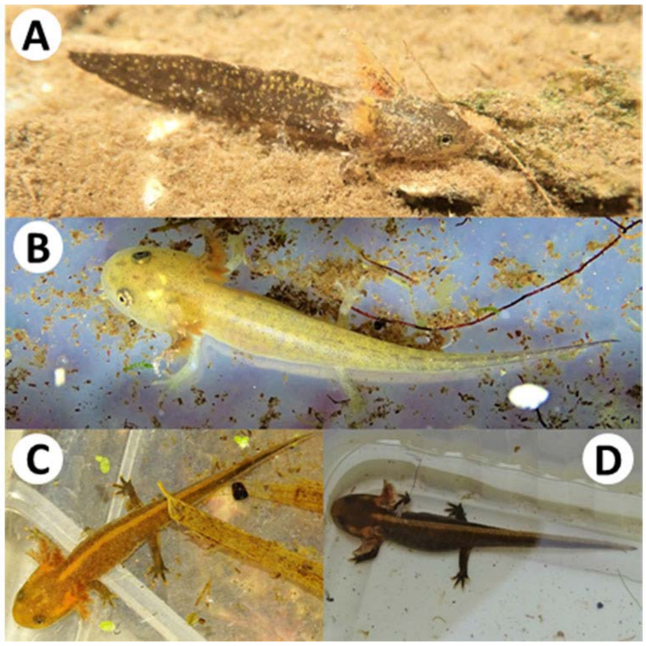

Figure 4. Larval development of *T. panhai*- **A.** At 15 days **B.** At 45 days, **C.** At 65 days, **D**. At 95 days

Egg laying and hatch rate

On June 26th 2020 at 22:35 h with water temperature of 21 °C, the first adult female laid 43 eggs, followed two days later by the second female with 41 eggs. The eggs were deposited singly or in small clutches of 4-22 eggs. The eggs were attached under wet moss above the water throughout the terrestrial part of the aquaterrarium. Egg size ranged between 12.6 ± 0.4 mm (n=84) and the mean size of the embryo capsule 5.1 ± 0.1 mm (n=84). In shape the eggs were rounded and they contained a slightly clear gelatinous layer, with some eggs more opaque in colouration. The liquid inside was very clear. The capsular chamber contained an embryo that was a noticeably dark to brownish or with a creamy yellowish to whitish colouration (Fig. 1C). About 80 % of the eggs hatched successfully.

Larval development and morphological characters

Diagnostic morphological characters for larvae are provided for stages 30-46 (see Fig. 4) following Grosse (1997). On 3rd July, 7-9 days after hatching at a water temperature of 19 °C the 67 larvae that had survived were at stages 30-32 and were observed on the bottom of the aquaterrarium. The range in total length of these 67 larvae was 11.89-13.78 mm. The dorsal fin was well-developed and higher than the head, starting at the middle of the trunk; the ventral fin shorter than dorsal fin. When hatching, larvae were thin, long and very slender in appearance; snout short and flat; ground colouration yellowish with a dense dark pigmentation on the whole body; gills well-developed and yellowish to pale orange different colouration, especially on their extremities. At 10-15 days, two fingers were visible on the forelimb of some larvae (stage 33; n=10), while in others the hind limb bud (stage 37; N=10) was already noticeable. At 17-22 days, all four fingers, five toes and joints were fully developed after (stage 43; n=10). At 45-75 days, larvae were totally vivid yellowish to bright orange in appearance with numerous and various dark little spots on the dorsal parts and red gills were slightly high (stage 44; n=10). At 65-95 days, pigmentation was darker turning to black and gills starting to degenerate (stage 45; n=10). At 75-99 days, red gills disappeared (stage 46; n=10). Larvae were fully developed and dark in colouration. Metamorphosis was completed by 99-102 days and efts started to move to land at an average total length of 56.2 mm and their weight range was 0.6-0.9 g (n=12). The general ground colouration was dark to black on the dorsal parts, tail, venter and head with a pure orange to yellowish orange colouration on parotoids, mouth area and snout, vertebral ridge, tips of fingers and toes as well as ventral ridge of tail; the eyes were golden with black pupils. By 127 days, juveniles developed an orange colouration on the 9-12 dorsolateral glandular warts, reaching an average snout-vent length of 75 mm (n=12).

DISCUSSION

Under natural conditions, adult *T. panhai* enter water at the end of April to early May and remain there until August during the monsoon season, which corresponds to the breeding period (Pomchote et al., 2008). Both males and females of the species develop an attractive and brighter colouration for their nuptial dance, becoming lighter in appearance as observed in other *Yaotriton* relatives such as *Tylototriton asperrimus* (Hernandez, 2016b). According to Khonsue et al. (2010), wild *T. panhai* can reach sexual maturity at 4-8 years in males (n=12) and 4-6 years in females (n=2). Our study corroborates these results and confirms that the captive specimens were more than six years old at first reproduction.

The various species within the genus *Tylototriton* differ in reproductive behaviours to the extent that there can be either terrestrial or aquatic mating and there are variations in the sites they select for oviposition (Pogoda et al., 2020). In this study, the breeding behaviour of *T. panhai* involved five main stages including i/approach, ii/nuptial dance, iii/amplexus, iv/spermatophore deposition, and v/fertilisation. Similar stages were previously reported in other related species within the subgenus *Yaotriton* in the wild including *T. wenxianensis* (Sichuan province), *T. asperrimus*, and *T. lizhenchangi* (Raffaëlli, 2013; Sparreboom, 2014; Hernandez, 2016b). Within the subgenus *Liangshantriton*, studies in the wild of *T. pseudoverrucosus* and *T. taliangensis* have shown that they employ ventral amplexus (Hernandez, 2018) of the type used by *T. panhai*.

The two females of *T. panhai* deposited a total of 84 eggs with egg viability of about 80 % indicating this species may breed successfully in captivity. The current study confirms previous reports that the species deposits eggs singly but mostly in small clutch of 10-20 eggs on land, particularly in moss with a saturated wet atmosphere (Hernandez, 2016b). Hernandez & Pomchote (2020) reported oviposition sites being on land near ponds, where eggs were attached to twigs, plants and even grasses or tree roots, sometimes more than 20–40 cm above the ground to avoid predators. Thus, *T. panhai* shows a preference for terrestrial oviposition while other congeners among the subgenera *Tylototriton* and *Liangshantriton* mainly lay their eggs in water bodies (Pogoda et al., 2020).

Eggs of *T. panhai* are remarkably large in size and the description of the egg and its embryo is very similar to that of its sister species *Tylototriton vietnamensis* (Bernardes et al., 2017). This study shows that an adult female may deposit a total of 4-43 eggs measuring 12.6 mm, values that are similar to our field observations of this species (Hernandez & Pomchote, 2020); female *T. vietnamensis* may deposit a total of 5-85 eggs, measuring 6.06-13.58 mm (mean 9.73 ± 1.61 mm; n=133), deposited either singly or in small clutches between 17 and 188 cm (mean 80 ± 41 cm; N=41) from water bodies (Bernardes et al., 2017). Our observations from captive and wild specimens are congruent with most of other species within the subgenus *Yaotriton* depositing an average of 20-99 eggs on land, mainly in clutches or, even singly as previously reported by Fei and Ye (2016).

Larvae are of the pond-dwelling type with red gills and feed on various invertebrates (Hernandez, 2016c). Their total length 7-9 days post hatching was 11.89-13.78 mm (n=67) and metamorphosis was completed after 99-102 days. Efts started to move to land at an average total length of 56.2 mm (n=10). Certain species of salamander exhibit breeding behaviours and phenology that diverge widely from those of wild populations (Bernardes et al., 2017) and this remains an important area for future study of *T. panhai*.

The current study provides new insights into the reproduction of *Tylototriton* in captivity. The subgenus *Tylototriton* including the species complex, *T. verrucosus* and *T. shanjing*, was the first species group to breed in captivity with successful results recorded for many years (Mudrack, 1969; Ziegler et al., 2008). During the last decade, several new species have also reproduced in captivity including *T. yangi*, *T. shanorum*, *T. kweichowensis*, *T. lizhenchangi*, *T. vietnamensis*, *T. ziegleri*, *T. wenxianensis* and *T. taliangensis* (Raffaëlli, 2013; Pasmans et al., 2014; Sparreboom, 2014). Studies have shown that in long-term captivity, reproduction may fail in many species but may be successful if the captive newts are in a large aquaterrarium and provided with a dry and cool period from October to April-June and a wet, moist and warmer period from April to August (Raffaëlli, 2013). The first attempts to induce breeding were to keep the newts indoors and then to introduce a homemade rain chamber into the aquaterrarium at the right moment. This approach was superseded by the use of an aquaterrarium with a larger aquatic section that was placed outdoors in a wet and poorly illuminated location (Hernandez, 2016b,c). In this study, we used the second approach which involved providing a large aquaterrarium of 200 x 60 x 60 cm placed outdoors during several rainy days in June, the water at pH 6.3-7.2 and temperatures varying from 24 °C in the day to 18 °C at night.

Although the morphology of the newts investigated in this study is congruent with *T. panhai* (phenotype II), without collection locality or published genetic data, there remains the possibility that the data pertain to another (potentially undescribed) species. Such issues have arisen previously, for example an in almost identical husbandry and breeding article (Sparreboom, 1984) where animals referred to as *Paramesotriton chinensis* were in reality *P. fuzhongensis* a species described 5 years after the publication of the article. In any case, the observations presented in this article represent a step forward in understanding the captive care and breeding of *Tyltotriton* spp. that can be employed in any future ex situ conservation programme. However, successful restocking programmes should have in mind the importance of genetic diversity for assuring long-term survival of the populations and must be paired with threat mitigation in the field (Browne et al., 2011).

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