SALAMANDRA **57**(1): 65–74
15 February 2021 | ISSN 0036–3375

SALAMANDRA
German Journal of Herpetology

Wild observations of the reproductive behaviour and first evidence of vocalization in Crocodile newt *Tylototriton himalayanus* (Caudata: Salamandridae) from the Himalayan biodiversity hotspot in Eastern India

Ajay Bedi[1]*, Vijay Bedi[1]*, Sarbani Nag[2] & Robin Suyesh[3]*

[1] Bedi Universal, D-28 Rajouri Garden, New Delhi, India
[2] We Initiate Socio-ecological Harmony Foundation, Kolkata, India
[3] Department of Environmental Sciences, Sri Venkateswara College, University of Delhi, Dhaula Kuan 110021, India
* These authors contributed equally to this work.

Corresponding author: Robin Suyesh, e-mail: robins@svc.ac.in

Manuscript received: 13 July 2020
Accepted 29 December 2020 by Stefan Lötters

Abstract. In this study, we provide the description of reproductive behaviour and also report the first evidence and description of vocalization in *Tylototriton himalayanus,* a recently described species from Eastern India and Nepal. Known variously as the Himalayan crocodile newt or orange-warted salamander, *T. himalayanus* is one of two known salamanders from the Himalayan Biodiversity hotspot in India. The study was conducted in the natural habitat of *T. himalayanus*, in Darjeeling district of West Bengal, during its breeding season. The observations were made in ephemeral ponds formed after the monsoon showers. Courtship behaviour and mating happened both during day and night. Operational sex ratio of the breeding population was skewed towards males as generally observed in amphibians. The males occupied the center of the pond and females were abundant on the periphery. Physical competition was observed among males for the possession of females. The courtship and amplexus lasts for about 90 min. After amplexus, the females laid about 1–9 eggs per oviposition site, and the entire egg laying process lasted for about 193 minutes. The males were also observed to produce very feeble and extremely rare 'ptaak' sounds, which either had pulsatile or non-pulsatile (single pulse) temporal structure. The in-situ observations recorded in the present study can play a significant role in devising effective conservation management plan for the species.

Key words. Amphibia, breeding, bioacoustics, conservation, Eastern Himalayas.

Introduction

The Indian Subcontinent has a rich assemblage of the amphibian fauna, especially anurans, but natural history of most of these amphibians is largely unknown (Gaitonde et al. 2016). Lately, few novel behavioural studies have been published on amphibians of Indian subcontinent, (Preininger et al. 2013, Gaitonde & Giri 2014, Gururaja et al. 2014, Seshadri et al. 2015, Crump 2015, Senevirathne et al. 2016, Willaert et al. 2016, Gaitonde et al. 2016) which elaborate upon the exceptional and phenomenal behavioural adaptation in the Indian amphibians along with the rich diversity. Amphibians are known for diversity in their reproductive strategies among all tetrapod vertebrates (Haddad & Prado 2005, Vitt & Caldwell 2013). A proper understanding of the reproductive biology is imperative for the conservation of the species and its habitat.

Salamanders or caudates are a group of amphibians comprising of 762 species, which are predominantly distributed in the prehistoric Laurasian landmass (AmphibiaWeb 2020, Frost, 2020). The Indian subcontinent, which was historically part of the Gondwana land, consists of only two species, *Tylototriton himalayanus* and *T. verrucosus,* which inhabit the Himalayan Biodiversity Hotspot in North-Eastern India (Khatiwada et al. 2015). Studies have suggested that these caudates might have arrived on the Indian subcontinent following the collision of drifting Indian plate with Asia about 34 million years ago (Aitchison et al. 2007), which assisted the biological exchange between Indian subcontinent and Asia (Bossuyt et al. 2006, van Bocxlaer et. al. 2009). *Tylototriton himalayanus*, commonly called as Himalayan crocodile newt, was recently differentiated from *T. verrucosus,* and described as a novel taxon having its distribution in Eastern India and Nepal (Khatiwada et al. 2015). The study species is predominantly found in temporary water pools, marshes and slow-moving drainage, which are formed after the arrival of the monsoon in their natural habitat.

Several attempts have been made in the past to understand the breeding biology of *T. himalayanus* (studied as *T. verrucosus* in Dasgupta 1984, Shrestha 1989, Kuzmin et al. 1994, Roy & Mushahidunnabi 2001, Deuti & Hegde 2007, Nag & Vasudevan 2014). However, the behavioural observations that have been reported in most studies have been conducted in laboratory or captive conditions, which may have differences when compared to natural conditions (Dasgupta 1984, Shrestha 1989, Kuzmin et al. 1994, Roy & Mushahidunnabi 2001). Although there are few reports of reproductive behaviour in natural conditions but it lacked detailed description and evidences to support the observations (Deuti & Hegde 2007, Nag & Vasudevan 2014). The precise nature of the mating system of these salamanders can only be understood by making observations in the wild (Verrel 1989, Wells 2010).

Among anuran amphibian vocalization is one of the most important and conspicuous feature to perform social interactions during the breeding season (Wells 2010). In contrast to anuran amphibian, vocalization is uncommon in caudates, and is not known to play any significant role in its mating strategy (Duellman & Trueb 1984, Wells 2010). Interestingly, two of the earlier study mentions this species to be vocalizing but it lacked recording or description of calls (Shrestha 1989, Deuti & Hegde 2007). In this study, we describe the reproductive strategy of *T. himalayanus* in the wild and also provide the first evidence of vocalization in them. The current study can be a rich source for generating and testing new hypothesis on these animals.

Materials and methods

Study site

The study was conducted in Nakapani in Mirik, Darjeeling District, West Bengal (88°8'56.4" N and 26°55'4.8" E) at an altitude of 1,620 m asl. The main monsoon period lasts from June to September with average rainfall of about 2,080 mm. Field work was conducted after the pre-monsoon showers from 21 May 2015 to 15 June 2015. The dry period after the pre monsoon showers lasted for 12 days, which also resulted in drying up of the study sites. The monsoon showers happened from 7 June 2015. The study area mostly had overcast condition all throughout the day. The daily average temperature at the study site during the study period was 18.6°C (17.2–21.3°C). The humidity level at the study site varied between 73–100%.

The breeding sites in the current study were shallow ephemeral ponds around a tea estate. These seasonal ponds were formed at the junction of hillocks after the monsoon rains. Ephemeral ponds serve as extremely productive habitats for salamanders, as its semi-annual nature prevents the establishment of predators e.g. fishes (Powell & Babbitt 2015). The ponds predominantly had the following aquatic vegetation, *Acorus calamus* (Bojho in Nepali), *Polygonum* sp. (Peeray Jhar in Nepali), *Nasturtium officinale* (Watercress in English; Simrayo in Nepali). Watercress was mostly preferred as the substrate for egg laying. The breeding site near human habitation was slow moving drainage from houses which had some weeds known as Gagleto (Nepali), which was used as substrate for egg laying.

Observational study

The observations were conducted in three seasonal ponds in the tea plantation. The dimensions of the ponds were 12 × 7.5 × 0.6 m, 8 × 5.5 × 0.9 m and 3.6 × 1.8 × 0.5 m (each length, breadth and depth) . The study sites were close to each other and they were within an area of 2 km². The study sites were separated by tea plantation, forest patches, roads and human settlements. The distance from the nearest human settlement ranged between 0.3–0.5 km. Observations were also made in a drain in the human settlement.

The observations were made between 18:00–12:00 h (evening of a day to noon of next day) everyday. Eight courting pairs were monitored during the study. Each pair was observed from starting from the time it was first spotted until the female left the oviposition site after egg laying. The time duration in minutes was noted for courtship behaviour, amplexus, free-swimming time of females (post amplexus) and oviposition. The measurement of snout to vent length (SVL) and total length (TL) of the males and females were taken for this study after oviposition. The SVL was measured from the tip of the snout to vent (cloaca) and for TL the measurement from vent to the tip of tail was added to SVL. The size of the egg with and without the jelly capsule was also measured. The measurements of SVL, TL and eggs were done using the slide calipers. The temperature and humidity was measured using Kestrel 3500 Weather Meter.

Sound recording and analysis

Two males were observed vocalizing during the entire study period. The male *T. himalayanus* produced 'ptaak' sounds that were rare, very feeble and extremely difficult to record. The recordings were made using Panasonic GH4 camera mounted with DXA-SLR ultra adapter and Sennheiser ME 416 directional microphone. The microphone was placed approximately 1m from the vocalizing male. A total of three calls were recorded from two males (two calls from one male). The males were not disturbed after the recording as they were also a part of the breeding behaviour study. The sound analysis was done using Raven Pro v1.4 and terminology for acoustic signals were based on Bee et al. (2013 a, b). The quantitative analysis was done using MS Excel (v14.0).

Results

Sexual dimorphism and sex ratio

Sexual dimorphism was observed between the male and female salamanders (Fig. 1). According to the observation the female salamanders appeared to be larger than the males. The SVL and TL (total length) of the observed female salamanders was 94.1 ± 1.0 mm and 184.8 ± 3.7 mm, respectively, while for male salamanders it was 86.3 ± 3.6 mm and 157.2 ± 2.1 mm, respectively. Also, female salamanders appeared to be brighter in color compared to males (Supplementary Video S1). Moreover, protruding cloacal apertures were prominent in gravid females, while the protrusion was lacking in males. The males were predominantly seen at the center of the pond while the females were dominant at the edges of the pond. The operational sex ratio here was also male-biased with a ratio of 12:1 (average from the study sites) as generally seen in caudates (Halliday & Verrel 1984, Zuiderwik 1990).

Courtship behaviour and amplexus

The species was observed to be actively breeding both at night and during the daylight hours. The males were observed to be at the center of the ponds and females were sighted at the edge of the pond at all study sites. Males were seen swimming towards the edge of the ponds to approach a female. Upon encountering a female, the male salamanders were seen presenting their full lateral view of the body and tail to the female. The females were seen to move away if they were not interested in the approaching male. The interested female was seen to rub its snout against the belly of the approaching male. The pair was seen rotating in the clockwise direction (female pushing the male) (Figs 2A–D, Supplementary Video S2/A) and while rotating the male was observed to wag (fan) the tip of its tail towards the head of the female (Fig. 2C, Supplementary Video S2/B), presumably giving visual stimulus to the female. At the end the female gives a push to the male and goes under the male. The male was then seen lying upside down in submissive position over the still female for few seconds (Fig. 2E, Supplementary Video S2/C). The male then swims quickly going under the female and grabs the forelimbs of female with its forelimb forming an amplexus (ventral amplexus) (Fig. 2F, Supplementary Video S3).

Figure 1. Sexual dimorphism in *Tylototriton verrucosus*. Larger and brighter female vs. smaller and darker male.

Table 1. Descriptive statistics of *Tylototriton himalayanus* breeding behaviour, based on the information determined from the 8 studied courting pair. Shown here are the mean ($\bar{x}$), standard deviation (SD) and range of individual timings.

Breeding behaviour	$\bar{x}$	SD	range
Courtship time (min)	29.6	6.1	22–39
Amplexus (min)	62.5	9.2	51–75
Post-amplexus swimming time (female) (min)	28.3	8.6	21–45
Egg laying time (min)	193.4	51.1	125–255
Number of eggs	71.2	11.5	52–88

The entire courtship period lasted for 29.6 ± 6.1 min (Table 1). The pair moved around (swimming as well as resting) in amplected position around the pond. The amplexus lasted for about 62.5 ± 9.2 min (Table 1). In this species the fertilization is internal. The male released the sperm sacs during amplexus and the females sucked the sperm sac by opening its cloaca. The male's position below the female is important for the sperm sacs to be captured by females. An illustration of courtship behaviour and amplexus is shown by Figures 3A–E.

Oviposition

The pairs separate after the amplexus and the females were seen swimming freely post amplexus for 28.25 ± 8.6 min (Table 1). The females then moved toward the edge of the pond inside the vegetation cover to lay the eggs and females were seen laying 1–9 eggs per site (Figs 4 A–D). The clutch size ranged between 52–88 eggs in the observed study (Table 1). The entire egg laying process lasted for 193.4 ± 51.1 min (Table 1). Egg size ranged between 2.9 ± 0.2 mm (N = 50) and the mean size of the egg with jelly capsule 5.0 ± 0.3 (N = 50). A short video of female with eggs is provided as Supplementary Video S4. An illustration of oviposition is shown by Figures 3F–G.

Inter-male competition

Inter-male competition was observed in Himalayan crocodile newts. The males were constantly seen engaged in territorial fights at the center of the pond and were also seen attempting to stop other males from moving towards the edge of the pond towards a potential mate. During the territorial fights the males were often seen biting each other and were also seen running after the rival male salamander when it was trying to escape. Moreover, the males were observed trying to break amplected pairs by holding the female's hind legs and then attempting to enter in between the amplected pair (Fig. 5, Supplementary Video S5). Besides swimming around the pond, the amplected pairs were also seen climbing onto the rocks inside the pond to avoid interference by other rival males (Fig. 2 F).

Vocalization

Tylototriton himalayanus based on the three-recorded calls were observed to produce single type of call, which either had pulsatile or non-pulsatile (single pulse) temporal structure. Figure 6 illustrates an advertisement call of *T. himalayanus*. The males were observed calling while sitting on a piece of rock inside a shallow pond (Supplementary Video S6).

Advertisement calls (Figs 6A–B) ranged between 15–146 ms in duration (Table 2). The call rise time of was very short ($\bar{x}$ = 2.2 ± 0.9 ms), while call fall time was relatively longer ($\bar{x}$ = 69.0 ± 67.4 ms).

Two calls had pulsatile temporal structure with 2 pulses (both pulsatile calls were from different males) while one call had single pulse. The pulse rate varied considerably be-

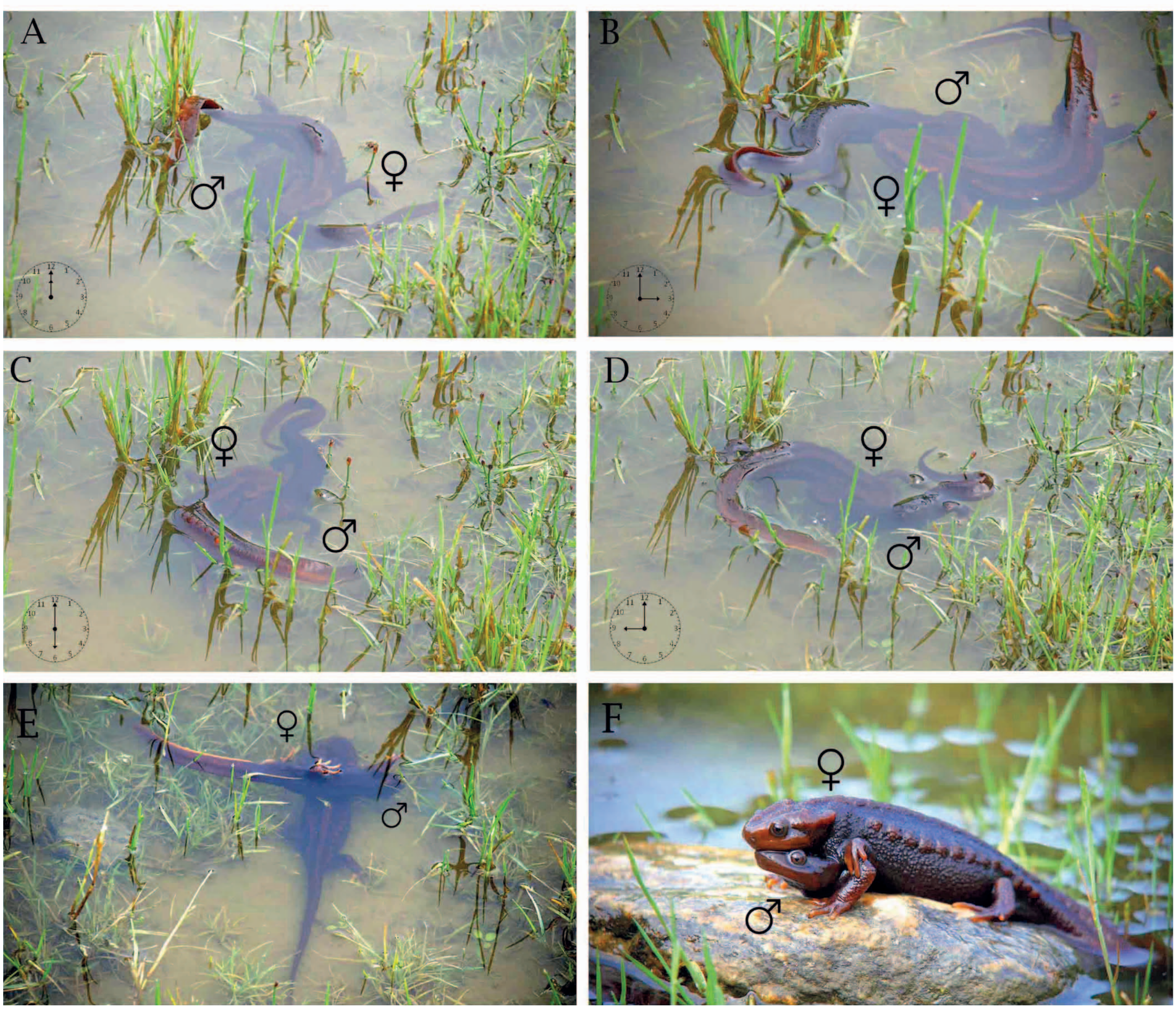

Figure 2. Courtship behaviour and amplexus in Himalayan Newts *Tylototriton verrucosus*. A–D) Pair rotating in the clockwise direction (female pushing the male), C) male wagging the tip of its tail towards the head of the female, E) male lying upside down in submissive position over the still female, F) male and female in ventral amplexus.

tween the two pulsatile calls (15.3 pulses/s and 52.7 pulses/s, respectively). The spectrum was characterized by single broad peak with low dominant frequency of 656.2 Hz (Fig. 6 C).

The individual pulses composing a call were about 17.2 ms in duration. Pulses had short rise time ($\bar{x}$ = 2.9 ms), with pulse reaching 50% of maximum amplitude in 1.4 ms. The pulse fall time ($\bar{x}$ = 14.3 ms) was nearly 5 times longer than the rise time. The pulse decreasing to 50% of its maximum amplitude was nearly 10.9 ms before the end of the pulse (Table 2).

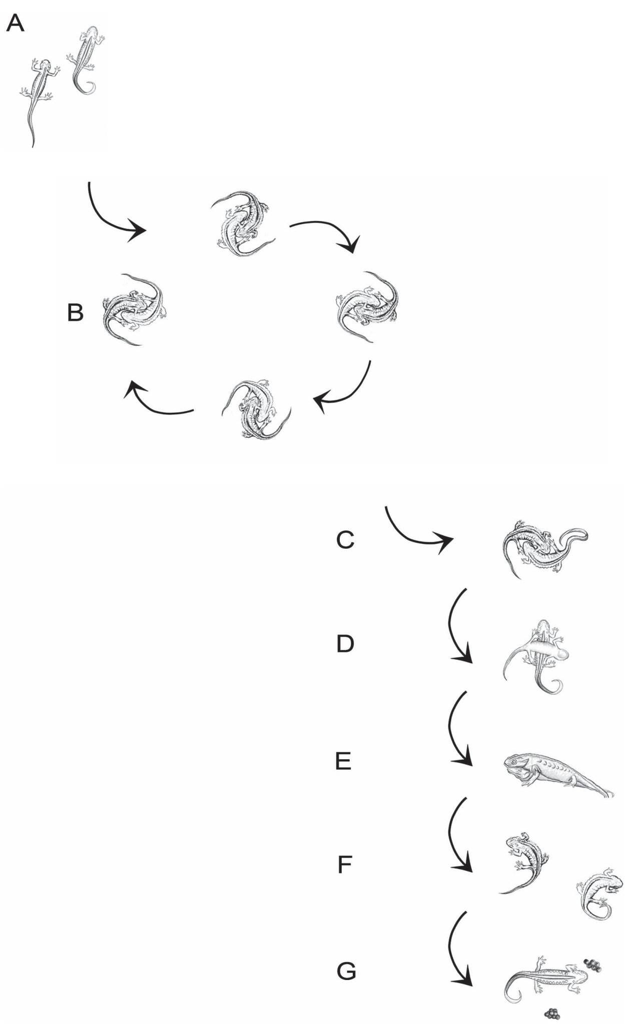

Figure 3. An illustration of reproductive behaviour in crocodile newt (*Tylototriton himalayanus*). A–E) Courtship behaviour and amplexus in Himalayan newts; A) male Himalayan newts approaching female (presenting their lateral view), B) male and female salamander rotating in clockwise direction (interested female rubs its snout and pushes the male), C) male wagging tip of its tail towards the head of the female, D) male lying upside down in submissive position over still female, E) male and female Himalayan newts engaged in ventral amplexus. F–G) Oviposition in Himalayan newts; F) male and female separate after amplexus, G) female Himalayan newts laying eggs at multiple sites.

Table 2. Description of male *Tylototriton himalayanus* advertisement calls, based on the values determined from a sample of 3 calls. Shown here are the mean ($\bar{x}$), standard deviation (SD) and range of individual means (* indicates median values).

Call properties	$\bar{x}$	SD	range
Call duration (ms)	72.0	67.1	15.2–146.1
Call rise time (ms)	2.9	1.0	2.2–4.0
Call fall time (ms)	69.1	67.1	12.7–143.8
Pulses per call*	2	–	1–2
Pulse rate (pulses/s)	34.1	26.8	15.4–52.8
Overall dominant frequency (Hz)	656.2	0	656.2–656.2
Pulse duration (ms)	17.3	2.1	15.3–19.4
Pulse rise time (ms)	2.9	1.0	2.2–4.0
Pulse 50% rise time (ms)	1.4	0.5	0.9–1.9
Pulse fall time (ms)	14.3	1.4	12.7–15.3
Pulse 50% fall time (ms)	11.0	1.7	9.8–12.9

Discussion

The current study is a comprehensive study on the breeding behaviour of Himalayan crocodile newts, *Tylototriton himalayanus* in the wild (observed during a single mating season). Also, the study provides the first description of the calls produced by these Himalayan newts, which is an uncommon behaviour in caudates (Wells 2010).

Sexual dimorphism and sex ratio

The female *T. himalayanus* were found to be larger compared to the male. In many species of caudates, fecundity selection favours females to have larger body size (Wells 2010). Also, in salamanders inter-male competition and female preference are predominant component of the reproductive strategy, as "operational sex ratio" (sexually active males to responsive females) is male biased (Halliday & Verrel 1984, Verrel & Krenz 1998, Malmgren & Enghag 2008). Our study also records higher number of males compared to females at the breeding site. The observation is similar to what has been reported in *T. podichthys* from Laos and *T. verrucosus* (two populations, Toebisa and Kazhi) from Bhutan (Wangyal & Gurung 2012, Phimmachak et al. 2015), while equal sex ratio was observed for *T. verrucosus* at one locality (Kabjisa) in Bhutan (Wangyal & Gurung 2012). For, *T. shanjing* the sex ratio varied across the breeding season with more males observed during early and late parts of breeding season and more females were encountered during the middle of the breeding season (Jun et al. 2012).

Breeding behaviour

Tylototriton himalayanus are observed to perform their courtship behaviour by visual communication. Visual sig-

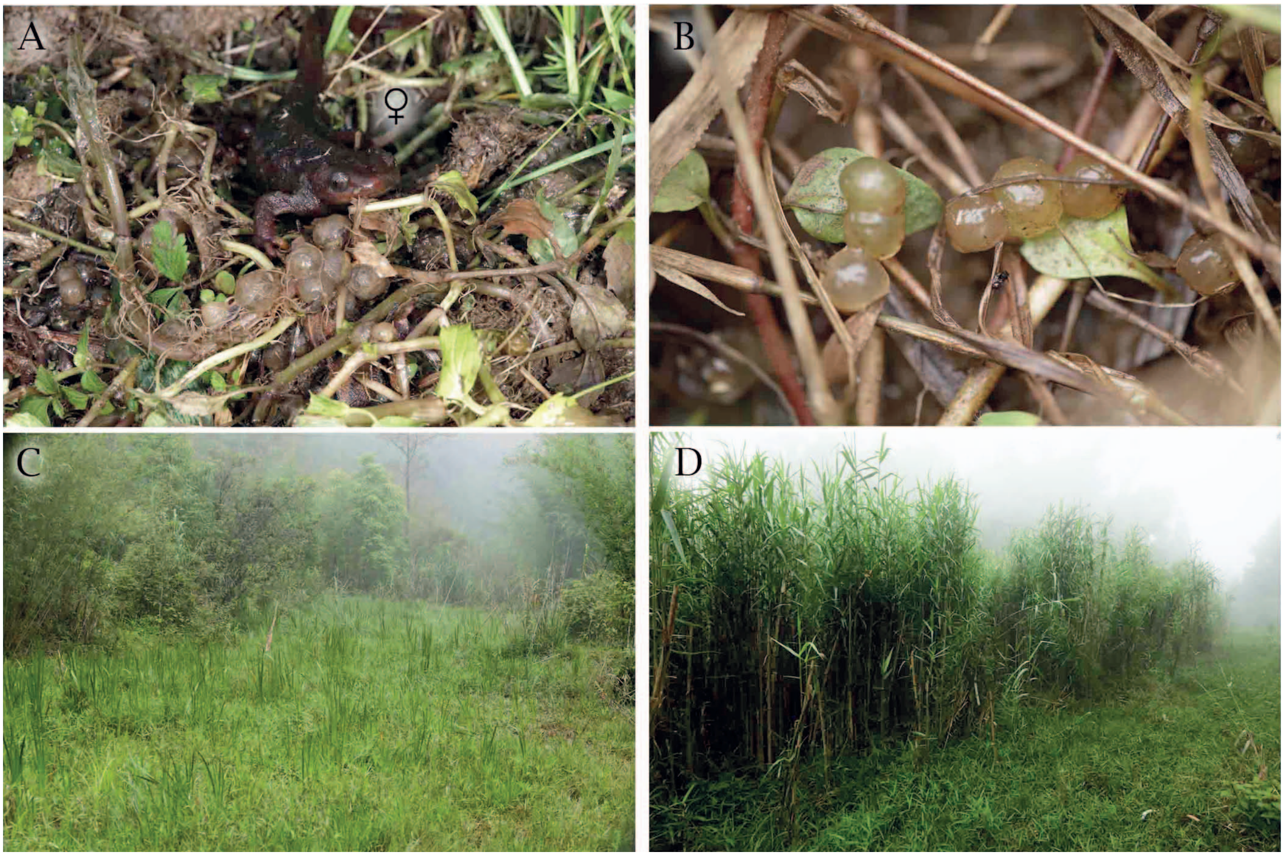

Figure 4. Oviposition in Himalayan Newts *Tylototriton verrucosus*. A) Female with eggs during oviposition, B) eggs attached to the substrate vegetation, C–D) oviposition sites at the edge of the breeding pond.

naling mechanism for courtship is commonly seen in the salamandrids, especially newts, which can be active both at night and daylight hours (Wells 2010). In *T. himalayanus,* the females were seen to rub the belly of the selected male by her snout. This behaviour has also been reported in *T. yangi* (in captivity) and it is more extensive compared to *T. himalayanus* (Wang et al. 2017). Also, Wang et al. (2017) suggested that rubbing behaviour could serve as a mechanism to obtain the olfactory information from the mate but further studies are required to understand the exact function of this behaviour within the genus *Tylototriton*.

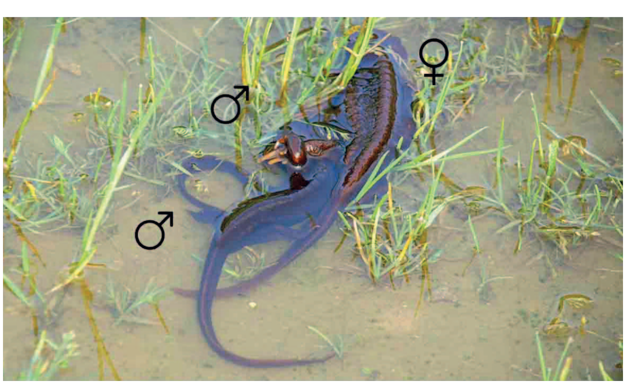

Figure 5. Inter-male competition. A male Himalayan newt attempting to break the amplexus of the mating pair.

The male courtship behaviour of *T. himalayanus* seemed similar to behaviour observed in *Lissotriton vulgaris* (Wells 2010). In *Lissotriton vulgaris*, the males have three types of courtship display (a) wave display – male holding its tail to present the female its full side view of tail; (b) whip – precipitous movement of male's tail towards its body intended to direct blasts of water towards female; (c) fan – subtle tail movement that direct a current of water towards female, also observed in *L. helveticus* and *Ichthyosaura alpestris* (Halliday 1977). The first and the third courtship display of *L. vulgaris* were similar to what was observed in *T. himalayanus*. Congeneric relatives, *Tylototriton kweichowensis*, *T. taliangensis, T. pseudoverrucosus, T. yangi* and *T. shanjing* also do tail fanning during their courtship behaviour (Wang et al. 2017). In another species, *Rhyacotriton olympicus,* the males have also been observed to wag the tip of its tail to provide visual stimulus to females (Arnold 1977).

During the amplexus, the males position themselves below the females (ventral amplexus). Along with genus *Tylototriton*, this type of amplexus is also observed in genus *Echinotriton* and *Pleurodeles* (Halliday 1990). Among the members of genus *Tylototriton*, the species *T. kweicho-*

wensis, *T. taliangensis* and *T. pseudoverrucosus* shows presence of ventral amplexus, while the species *T. yangi* and *T. shanjing* lacks ventral amplexus (Wang et al. 2017). Post amplexus, the females were observed to lay eggs at multiple sites. Though no egg predation was observed during the study, the deposition of eggs at multiple sites by females could potentially ensure better hatching success in these salamanders (Refsnider & Janzen 2010).

Our eight observations of courtship, amplexus and egg laying behaviour were after the monsoon showers. The salamanders also bred after the pre-monsoon showers, as the eggs were found attached to the vegetation around the ponds. There was a dry spell for about twelve days after the pre monsoon showers, which caused all the eggs laid initially to desiccate.

Vocalization

Unlike anurans, acoustic communication is not known to play any role in salamanders and they are considered to be 'silent' amphibians. However, few species of salamanders have been observed to produce a low intensity sound but the exact functions of these sounds is mostly unknown

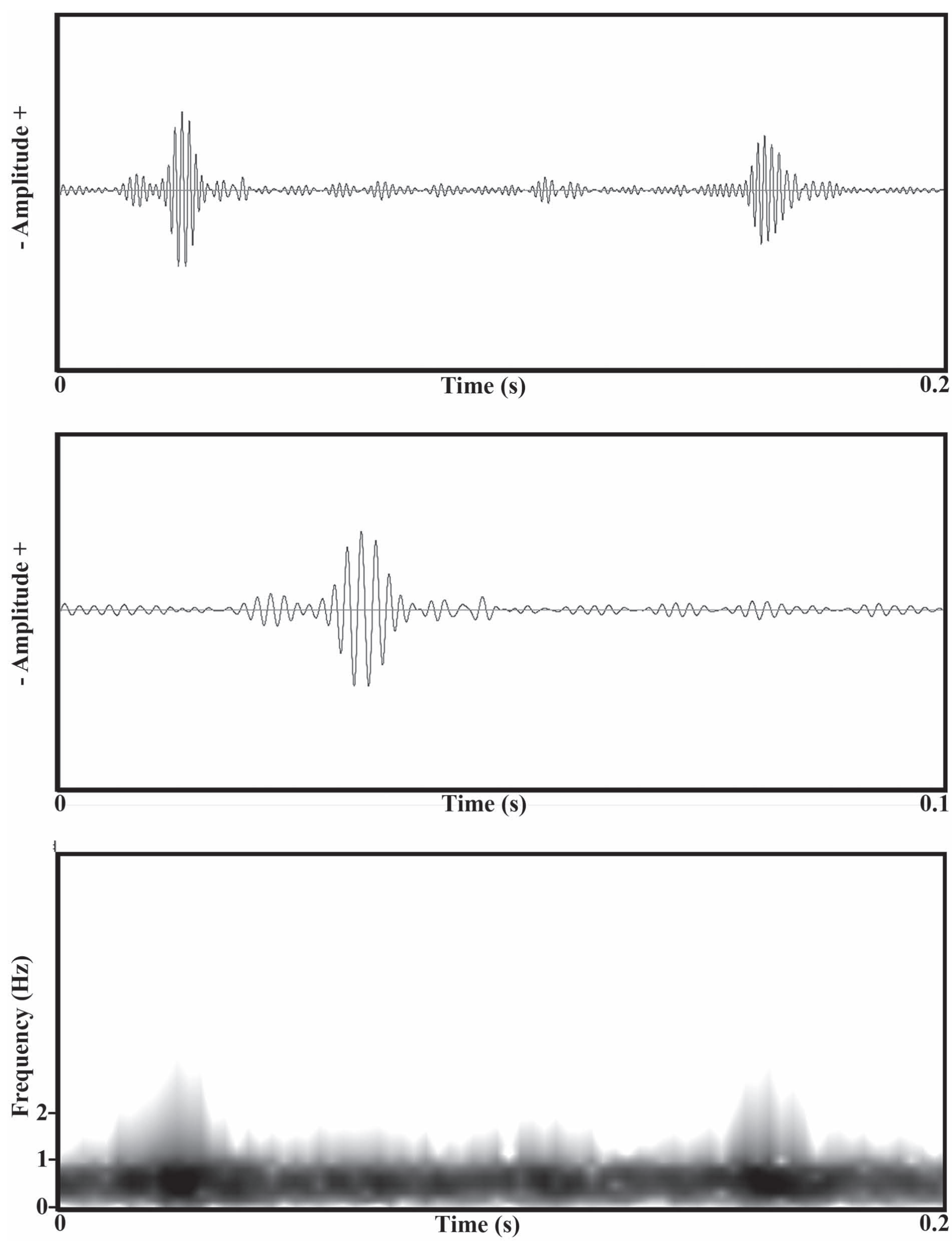

Figure 6. Oscillograms (above) and Spectrogram (below) of *Tylototriton himalayanus* calls. Top: 0.2 second segment showing the pulsatile call of *T. himalayanus*. Centre: 0.1 second segment showing single pulse. Bottom: spectrogram of 0.2 second call segment.

Figure 7. Conservation issues of Himalayan newts (*Tylototriton verrucosus*). A) Habitat destruction for housing projects, B) oil spills during cleaning of vehicles.

(Wells 2010). Salamanders have been observed to produce sound during sexual interaction, aggressive interaction between males and for defense against predators (Davis & Brattstrom 1975). The species, *Ambystoma maculatum, Eurycea bislineata, Salamandra salamandra, Taricha torosa* were witnessed to produce sound during sexual interaction (Bogert 1960, Wyman & Thrall 1972, Davis & Brattstrom 1975). *Ambystoma gracile, T. torosa, Plethodon vehiculum, Amphiuma means* have been observed to commonly produce sound during aggressive interaction between males (Licht 1973, Davis & Brattstrom 1975; Ovaska 1987, Crovo et al. 2016), while in *Dicamptodon ensatus*, *Aneides lugubris*, *A. texanum* the sound production is associated with anti-predatory defense mechanism (Maslin 1950, Bogert 1960, Coleman 2016). However, the only attempted playback experiment by Wyman and Thrall (1972) on spotted salamander *Ambystoma maculatum*, failed to show any response.

Although salamanders lack external ears (Jaslow et al. 1988), they can detect low frequency sounds below 1 kHz (Ross & Smith 1978, Wever 1985). A study by Diego-Rassila & Luengo (2002) showed that terrestrial marbled newts *Triturus marmoratus* use breeding choruses of *Bufo calamita* to locate suitable breeding pools, which clearly indicates even better terrestrial hearing capacity for salamanders. The study species, *T. himalayanus* was also observed to produce low frequency call (656 Hz). Deuti & Hedge (2007) mentioned these calls as mating calls but we did not observe any role of vocalization in breeding behaviour. Thus, the exact function of these calls still remains ambiguous and further studies will be required to understand its role.

Conservation

Currently the species is known from Himalayan region in the Indian states of West Bengal and Sikkim, and also from Eastern Nepal (Khatiwada et al. 2015). Due to various anthropogenic activities, the species currently face various threats such as siltation in ephemeral ponds (Seglie et al. 2003, Nag & Vasudevan 2014), destruction of host plants as fodder for domestic animals, household waste leading to eutrophication, road kills, introduction of invasive species (Kuzmin et al. 1994), exploitation for traditional medicine (Shrestha 1989), pesticide pollution and detergent in the water bodies (Shrestha 1989), oil spills and also by rampant habitat destruction for housing projects and plantation (Fig. 7; Supplementary Video S7). The species is currently classified as least concerned (as *Tylototriton verrucosus*) by IUCN (van Dijk et al. 2009), the conservation status need to be updated and serious efforts are required to create awareness among locals as the above activities may have caused a significant decline in their population.

Conclusion

Our study on *T. himalayanus* gives elaborate description of their reproductive behaviour in the wild, a species that prefers breeding after the onset of peak monsoon in their habitat. The study also provides the first evidence of vocalization in this species, a behaviour that is uncommon in salamanders. Caudates do not show high diversity in the Indian sub-continent (AmphibiaWeb 2020, Frost 2020), which makes *T. himalayanus* a unique taxon from the Himalayan Biodiversity Hotspot of India. As the species is currently threatened by various anthropogenic activities, a proper understanding of their ecology, especially their reproductive behaviour is important for planning and implementing conservation action plans.

Acknowledgements

We are grateful to Mr. Ramesh Gazmere (Teacher, Thurbo School), other staff and students of Thurbo School, Untuk for their assistance in the field. We thank Nakapani Tea Estate, Thurbo Tea Estate and inhabitants of Mirik for their hospitality and support while conducting the field study. We are also grateful to Mr. Binit Priyaranjan for his support in editing. We are also thankful to Forest Department of West Bengal for their permission to film the salamanders.

References

Aitchison, J. C., J. R. Ali & A. M. Davis (2007): When and where did India and Asia collide? – Journal of Geophysical Research: Solid Earth, **112**: B5.

AmphibiaWeb (2020): AmphibiaWeb: Information on amphibian biology and conservation, – University of California, Berkeley, CA. – Available at http://www.amphibiaweb.org/, accessed 26 May 2020.

Arnold, S. J. (1977): The evolution of courtship behavior in New World salamanders with some comments on Old World salamandrids. – pp. 141–183 in: Taylor, D. (ed.): The reproductive biology of amphibians. – Springer, Boston, MA.

Bee, M. A., R. Suyesh & S. D. Biju (2013a): Vocal behavior of the Ponmudi Bush Frog (*Raorchestes graminirupes*): repertoire and individual variation. – Herpetologica, **69**: 22–35.

Bee, M. A., R. Suyesh & S. D. Biju (2013b): The vocal repertoire of *Pseudophilautus kani*, a shrub frog (Anura: Rhacophoridae) from the Western Ghats of India. – Bioacoustics **22**: 67–85.

Bogert, C. M. (1960): The influence of sound on the behavior of amphibians and reptiles. – American Institute of Biological Sciences, Washington D. C.

Bossuyt, F., R. M. Brown, D. M. Hillis D. C. Cannatella & M. C. Milinkovitch (2006): Phylogeny and biogeography of a cosmopolitan frog radiation: late Cretaceous diversification resulted in continent-scale endemism in the family Ranidae. – Systematic Biology **55**: 579–594.

Coleman A. (2016): Sound production in the small-mouthed salamander (*Ambystoma texanum*). – Unpubl. Masters Thesis, Emporia State University, Emporia, KS.

Crovo, J. A., J. N. Zeyl & C. E. Johnston (2016): Hearing and sound production in the aquatic salamander, *Amphiuma means*. – Herpetologica, **72**: 167–173.

Crump, M. L. (2015): Anuran reproductive modes: evolving perspectives. – Journal of Herpetology **49**: 1–6.

Davis, J. R. & B. H. Brattstrom (1975): Sounds produced by the California newt, *Taricha torosa*. – Herpetologica. **1**: 409–412.

Dasgupta, R. (1984): Parental care in the Himalayan newt. – Journal of Bengal Natural History Society, New Series **3**: 106–109.

Deuti, K. & V. K. Hegde (2007): Handbook on Himalayan Salamanders. – Nature Books India, New Delhi.

Diego-Rassila, J. F. & R. M. Luengo (2002): Celestial orientation in the marbled newt (*Triturus marmoratus*). – Journal of Ethology **20**: 137–141.

Duellman, W. E. & L. Trueb (1986) Biology of amphibians. – Johns Hopkins University Press, Baltimore, MD.

Frost, D. R. (2020): Amphibian species of the world: an online reference. Version 6.0: – American Museum of Natural History, New York, NY. – Available at http://research.amnh.org/herpetology/ amphibia/index.html, accessed 26 May 2020.

Gaitonde, N. & V. Giri (2014): Primitive breeding in an ancient Indian frog genus *Indirana*. – Current Science, **107**: 109–112.

Gaitonde, N., V. Giri & K. Kunte (2016): 'On the rocks': reproductive biology of the endemic toad *Xanthophryne* (Anura: Bufonidae) from the Western Ghats, India. – Journal of Natural History, **50**: 2557–2572.

Gururaja, K. V., K. P. Dinesh, H. Priti & G. Ravikanth (2014): Mud-packing frog: a novel breeding behaviour and parental care in a stream dwelling new species of *Nyctibatrachus* (Amphibia, Anura, Nyctibatrachidae). – Zootaxa, **3796**: 33–61.

Haddad C. F. & C. P. Prado (2005): Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brazil. – BioScience, **55**: 207–217.

Halliday, T. R. (1977): The courtship of European newts: an evolutionary perspective. – pp. 185–232 in: Taylor, D. (ed.): The reproductive biology of amphibians. – Springer, Boston, MA.

Halliday T. R. (1990): The evolution of courtship behavior in newts and salamanders. – pp. 137–169 in: Lehrman, D., R. Hinde & E. Shaw (eds): Advances in the Study of Behavior. – Academic Press, New York, NY.

Halliday, T & P. A. Verrel (1984): Sperm competition in amphibians. – pp. 487–508 in: Smith, R. L. (ed.): Sperm competition and the evolution of animal mating systems. – Academic Press, New York, NY.

Jaslow, A. P., T. E. Hetherington & R. E. Lombard (1988): Structure and function of the amphibian middle ear. – pp. 69–91 in: Fritzsch, B., M. J. Ryan, W. Wilczynski, T. E. Hetherington & W. Walcowiak (eds): The evolution of the amphibian auditory system. – Wiley, New York, NY.

Jun, L. P., A. Z. Liu, X. H. Liu & J. Kai (2012): The breeding ecology of red knobby newts *Tylototriton shanjing*. – Chinese Journal of Zoology, **47**: 8–15.

Khatiwada J. R., B. Wang, S. Ghimire, K. Vasudevan, S. Paudel & J. Jiang (2015): A new species of the genus *Tylototriton* (Amphibia: Urodela: Salamandridae) from eastern Himalaya. – Asian Herpetological Research, **6**: 245–256.

Kuzmin, S. L., R. Dasgupta & E. M. Smirina (1994): Ecology of the Himalayan newt (*Tylototriton verrucosus*) in Darjeeling Himalayas, India. – Russian Journal of Herpetology, **1**: 69–76.

Licht, L. E. (1973): Behavior and sound production by the northwestern salamander *Ambystoma gracile*. – Canadian Journal of Zoology, **51**: 1055–1056.

Malmgren, J. C. & M. Enghag (2008): Female preference for male dorsal crests in great crested newts (*Triturus cristatus*). – Ethology Ecology & Evolution, **20**: 71–80.

Maslin, T. P. (1950): The production of sound in caudate Amphibia. – University of Colorado Press, Boulder, CO.

Nag, S. & K. Vasudevan (2014): Observations on overwintering larvae of *Tylototriton verrucosus* (Caudata: Salamandridae) in Darjeeling, Himalaya, India. – Salamandra, **50**: 245–248.

Ovaska, K (1987): Seasonal changes in agonistic behaviour of the western red-backed salamander, *Plethodon vehiculum*. – Animal Behaviour, **35**: 67–74.

Phimmachak, S., B. L. Stuart & A. Aowphol (2015): Ecology and natural history of the knobby newt *Tylototriton podichthys* (Cauadata: Salamandridae) in Laos. – Raffles Bulletin of Zoology, **63:** 389–400.

Powell, J. S. V. & K. J. Babbitt (2015): An experimental test of buffer utility as a technique for managing pool-breeding amphibians. – PLoS ONE, **10**:e0133642.

Preininger, D., M. J. Steigler, K. V. Gururaja, S. P. Vijaykumar, V. R. Torsekar, M. Sztatecsny & W. Hödl (2013): Getting a kick out of it: Multimodal signalling during male–male encounters in the foot-flagging frog *Micrixalus* aff. *saxicola* from the Western Ghats of India. – Current Science, **25:** 1735–1740.

Refsnider, J. M. & F. J. Janzen (2010): Putting eggs in one basket: ecological and evolutionary hypotheses for variation in oviposition-site choice. – Annual Review of Ecology, Evolution and Systematics, **41**: 39–57.

Ross, R. J. & J. J. Smith (1978): Detection of substrate vibrations by salamanders: inner ear sense organ activity. – Canadian Journal of Zoology, **56**: 1156–1162.

Roy, D. & M. Mushahidunnabi (2001): Courtship, mating and egg-laying in *Tylototriton verrucosus* from the Darjeeling district of the Eastern Himalaya. – Current Science, **25:** 693–695.

Seglie, D., D. Roy, C. Giacoma & M. Mushahidunnabi (2003): Distribution and conservation of the Himalayan Newt (*Tylototriton verrucosus*, Urodela, Salamandridae) in the Darjeeling District, West Bengal (India). – Russian Journal of Herpetology, **10**: 159–164.

Senevirathne, G., S. Garg, R. Kerney, M. Meegaskumbura & S. D. Biju (2016): Unearthing the fossorial tadpoles of the Indian dancing frog family Micrixalidae. – PLoS ONE, **11**: e0151781.

Seshadri, K. S., K. V. Gururaja & D. P. Bickford (2015): Breeding in bamboo: a novel anuran reproductive strategy discovered in Rhacophorid frogs of the Western Ghats, India. – Biological Journal of the Linnean Society, **114**: 1–11.

Shrestha, T. K. (1989): Ecological aspects of the life-history of the Himalayan newt, *Tylototriton verrucosus* (Anderson) with reference to conservation and management. – Journal of the Bombay Natural History Society, **86**: 333–338.

Van Bocxlaer, I., S. D. Biju, S. P. Loader & F. Bossuyt (2009): Toad radiation reveals into-India dispersal as a source of endemism in the Western Ghats-Sri Lanka biodiversity hotspot. – BMC Evolutionary Biology, **9**: 131.

Van Dijk, P. P., G. Wogan, M. W. N. Lau, S. Dutta, T. K. Shrestha & N. Q. Truong (2009): *Tylototriton verrucosus*. The IUCN Red List of Threatened Species. – IUCN, Gland. – Available at: http://dx.doi.org/10.2305/IUCN.UK.2004.RLTS.T59487A11934912.en, accessed 20 May 2020.

Verrell, P. A. (1989): The sexual strategies of natural populations of newts and salamanders. – Herpetologica, **1**: 265–282.

Verrell, P. A. & D. Krenz (1998): Competition for mates in the Mole Salamander, *Ambystoma talpoideum*: tactics that may maximize male mating success. – Behaviour, **135**: 121–138.

Vitt, L. J. & J. P. Caldwell (2013): Herpetology: an introductory biology of amphibians and reptiles. – Academic Press, New York, NY

Wang, K., Z. Yuan, G.Zhong, G. Li & P. A. Verrell (2017): Reproductive biology of *Tylototriton yangi* (Urodela: Salamandridae), with suggestions on its conservation. – Amphibian & Reptile Conservation, **11**: 33–43.

Wangyal, J. T. & D. B. Gurung (2017): The distribution of Himalayan newts, *Tylototriton verrucosus* in the Punakha-Wangdue Valley, Bhutan. – Journal of Threatened Taxa, **4**: 3218–3222.

Wells, K. D. (2010): The ecology and behavior of amphibians. – University of Chicago Press, Chicago, IL.

Wever, E. G. (1985): The amphibian ear. – Princeton University Press, Princeton, NJ.

Willaert, B., R. Suyesh, S. Garg, V. B. Giri, M. A. Bee & S. D. Biju (2016): A unique mating strategy without physical contact during fertilization in Bombay Night Frogs (*Nyctibatrachus humayuni*) with the description of a new form of amplexus and female call. – PeerJ, **4**: e2117.

Wyman, R. L. & J. H. Thrall (1972): Sound production by the spotted salamander, *Ambystoma maculatum*. – Herpetologica, **28**: 210–212.

Zuiderwijk, A. (1990): Sexual strategies in the newts *Triturus cristatus* and *Triturus marmoratus*. – Bijdragen tot de Dierkunde, **60**: 51–64.

Supplementary data

The following data are available online:

Supplementary Video S1. Sexual dimorphism: Male and female salamander showing sexual dimorphism.

Supplementary Video S2/A. Courtship behaviour: Male and female salamander rotating in clockwise direction.

Supplementary Video S2/B. Courtship behaviour: Male salamander wagging the tip of its tail.

Supplementary Video S2/C. Courtship behaviour: Male lying in submissive position over still female.

Supplementary Video S3. Amplexus: Male and female salamander engaged in ventral amplexus.

Supplementary Video S4. Oviposition: Female salamander with eggs.

Supplementary Video S5. Inter-male competition: Male salamander trying to break the amplected pair.

Supplementary Video S6. Vocalization: Male salamander producing sound.

Supplementary Video S7. Conservation: Threats faced by salamanders in their habitat.