

Development and metamorphosis of tadpoles of the non-native Bengal toad, *Duttaphrynus bengalensis*, in an urban wetland in Singapore

Michael Richard Crossland^{1*} & Sheau Fong Chan

¹School of Life and Environmental Sciences, The University of Sydney, NSW 2006, Australia; Email: michael.crossland@sydney.edu.au (*corresponding author)

Abstract. The larval development and metamorphosis of the non-native Bengal toad, *Duttaphrynus bengalensis*, in a small urban wetland in Singapore is described. Early-stage tadpoles (Gosner stage 26–27) were initially observed in a single pool within the wetland. Over subsequent days, the tadpoles dispersed and/or were displaced by the water current into adjacent connected pools. The tadpoles developed rapidly, and we first observed metamorphosing toads 18 days after our initial observation of stage 26–27 tadpoles. It is estimated that egg deposition to metamorphosis took 24–28 days, hatchling to metamorphosis took 23–26 days and stage 25 tadpole to metamorphosis took 19–21 days. The capacity for such rapid development would allow *Duttaphrynus bengalensis* to utilise many ephemeral waterbodies as breeding sites.

Key words. *Duttaphrynus melanostictus*, Anura, reproduction, larval period, urban habitat

Recommended citation. Crossland MR & Chan SF (2024) Development and metamorphosis of tadpoles of the non-native Bengal toad, *Duttaphrynus bengalensis*, in an urban wetland in Singapore. *Nature in Singapore*, 17: e2024042. DOI: 10.26107/NIS-2024-0042

INTRODUCTION

The Asian toad, *Duttaphrynus melanostictus* (formerly *Bufo melanostictus*), is a species complex widely distributed in South and Southeast Asia (Wogan et al., 2016; Othman et al., 2020; Jablonski et al., 2022). This toad is a human commensal species, with non-native populations having become established in numerous locations including Bali, Sulawesi, New Guinea, the Andaman and Nicobar Islands, Timor Leste, Maldives and Madagascar (Trainor, 2009; O’Shea et al., 2015; Wogan et al., 2016; Licata et al., 2020; Soorae et al., 2020). Additionally, stowaways have been intercepted at the border in Australia, New Zealand and South Africa, while escapees have been collected from the wild in the United Arab Emirates before they could establish a local population (Soorae et al., 2020). Although historically referred to as a single species, recent genetic analysis indicates that *Duttaphrynus melanostictus* consists of multiple distinct evolutionary clades with discrete distributions (Wogan et al., 2016; Othman et al., 2020; Jablonski et al., 2022). The population of this toad that occurs in Singapore is part of a clade recently identified as *Duttaphrynus bengalensis* (Jablonski et al., 2022). This clade is deeply divergent from other clades of the *Duttaphrynus melanostictus* complex, and is native to Bangladesh, India, Nepal and Pakistan but introduced to Indonesia, Malaysia and Singapore, likely via human-mediated pathways (Jablonski et al., 2022).

A number of previous studies have investigated aspects of the reproductive ecology of the *Duttaphrynus melanostictus* complex. Breeding is seasonal in climatically variable environments (Jørgensen et al., 1986; Ngo & Ngo, 2013; Fan et al., 2016; Gramapurohit & Radder, 2012) but occurs throughout much of the year in more climatically stable environments such as Singapore (Berry, 1964). Reproduction occurs in a variety of temporary and permanent aquatic habitats, in both still and slow-flowing water (O’Shea et al., 2015; Jayawardena et al., 2017; Kelly et al., 2023). Although predominantly laying eggs in freshwater, this toad has also been reported breeding in brackish water, and tadpoles can survive in water up to 0.75% salinity (Leong & Chou, 1999). Each female toad produces 1–2 egg clutches per year (Ngo & Ngo, 2013; Kelly et al., 2023), with each clutch containing up to 40,000 eggs that are deposited in long strings (Berry, 1964; Kelly et al., 2023).

The eggs take 24–36 hours to develop into hatchlings depending on water temperature (Fan et al., 2016; Saidapur & Girish, 2000, 2001; Kelly et al., 2023), with hatching reported to occur between Gosner stages 17–20 (Gosner, 1960; Saidapur & Girish, 2000, 2001; Karraker, 2011; Mogali et al., 2017). The hatchlings remain attached to the egg jelly for 4–5 days until they reach the free-swimming, feeding tadpole stage (stage 25; Saidapur & Girish, 2000; Karraker, 2011; Jayawardena et al., 2017). From this time onwards, the tadpole diet consists primarily of algae, phytoplankton and detritus (Saidapur & Girish, 2000; Karraker, 2011; Kelly et al., 2023). However, these tadpoles are opportunistic cannibals of conspecific eggs, tadpoles and metamorphosing individuals, as well as scavengers of carrion such as dead tadpoles and dead adult anurans (Mahapatra et al., 2017; Kelly et al., 2023).

Estimates of the time to complete metamorphosis in nature are surprisingly rare for this widely distributed species complex. In India, Mahapatra et al. (2017) reported the “metamorphosis period” in the wild was 18–20 days, while Saidapur & Girish (2001) stated that tadpoles “metamorphose” in 25–30 days. However, in both cases, it is unclear whether these estimates refer to time from egg deposition, time from the hatchling stage or time from the initial free-swimming tadpole stage (stage 25; Gosner, 1960). Recently, Köhler & Thammachoti (2023) demonstrated that *Duttaphrynus melanostictus* in Thailand can complete metamorphosis 21 days after egg laying. This latter study involved tadpoles from naturally laid eggs being raised in plastic containers at ambient room water temperature (30–33°C during daytime, 26–28°C at night) with regular water changes and feeding. Thus, while not an estimate of larval period in a natural waterbody, it does demonstrate the potential for very rapid larval development consistent with Mahapatra et al. (2017) and Saidapur & Girish (2001). The larval period of anuran tadpoles in general is well known to be a plastic trait strongly influenced by factors such as water temperature, density and presence of competitors and predators (Alford, 1999). For *Duttaphrynus melanostictus*, laboratory studies have shown that tadpoles metamorphose faster in the presence of desiccation threat (Mogali et al., 2017) and when reared with kin with which they preferentially associate (Saidapur & Girish, 2000, 2001).

Singapore is home to at least 29 anuran species (Figuroa et al., 2023), with *Duttaphrynus bengalensis* being widespread and abundant, occurring in all habitat types including human settlements, urban areas and agricultural landscapes (Baker & Lim, 2012; Figuroa et al., 2023). The urban landscape of Singapore contains many small parks, and *Duttaphrynus bengalensis* is commonly found in even the smallest of such parks (Bickford et al., 2010). In this paper, we document the development of *Duttaphrynus bengalensis* tadpoles to metamorphosis in one such park.

MATERIAL & METHODS

Between 2–22 July 2023, we visited a constructed wetland adjacent to the Kong Meng San Phor Kark See Monastery, Singapore (01°21'42"N, 103°50'14"E). At the time of our visits, this publicly accessible wetland was approximately 190 m in length with a width ranging from 2.5–30 m (measured from Google Earth image using ImageJ; Schneider et al., 2012; Fig. 1). The wetland consisted of a series of eight pools. The top pool (assigned by us as pool 1) was connected to pool 2 by a waterfall ~1 m high. Pools 2–6 were connected by shallow riffles and runs, while pool 6 was connected to pool 7 by a waterfall ~1 m high and pool 7 was connected to pool 8 by a waterfall ~2 m high. The wetland held permanent water which flowed downstream via water pumped from underground into pool 1. Pools 1–5 had clear water with excellent visibility, while pools 6–8 had higher turbidity but still retained good water visibility within 0.5–1 m of the waters' edge. In late July 2023 (after we completed our observations), the wetland was closed to the public for construction works and remains closed as of 1 April 2024. It is not known to what extent the renovated wetland will differ in configuration from the wetland where we made our observations.

We made day-time visits to the wetland between 1700–1830 hours on 2 July, 9 July, 16 July and 20 July 2023. On each visit, we slowly walked around the perimeter of the entire wetland, looking into the water for aquatic life. We also looked for any diurnally active metamorph anurans within 2 m of the edge of the entire wetland. The grass at the wetland was maintained at a very low height, making it possible to look for metamorphs without physically searching through vegetation.

When we saw tadpoles, we slowly walked to the water's edge to observe the tadpoles at a distance of ~30 cm. The tadpoles did not appear to be disturbed by our presence as we did not observe any tadpoles flee when we approached. We photographed tadpoles in situ but did not handle them. We were able to estimate the developmental stage of tadpoles (Gosner, 1960) by visual observation because one of us (MRC) has more than 15 years' experience using Gosner (1960) to assess the developmental stage of thousands of similar-sized tadpoles of a related bufonid (the cane toad, *Rhinella marina*).

We also made night-time visits to the wetland between 2000–2130 hours on 21–22 July 2023 to look for terrestrial anurans using spotlights. We photographed several individuals but did not handle any anurans we observed.

We obtained daily rainfall data for the period 2–20 July 2023 from records for the nearest weather station (Ang Mo Kio weather station, <http://www.weather.gov.sg/climate-historical-daily/>).



Fig. 1. Wetland in Singapore where the observations were made. (Photograph by M. R. Crossland).

RESULTS

On 2 July 2023, we observed several hundred early development stage tadpoles (stage 26–27) in the second uppermost pool (pool 2). The tadpoles were mainly distributed along the edge of the pool and were either feeding on algae or were stationary (resting on the substrate or algae). The tadpoles were recognisable as *Duttaphrynus bengalensis* due to their jet-black dorsal skin colouration, clear tail fins, aggregation behaviour and general bufonid tadpole body shape (Leong & Chou, 1999; Chan & Goh, 2010). Given the number of tadpoles, their consistency in developmental stage and the known large clutch size for *Duttaphrynus bengalensis* (Berry, 1964), we consider these tadpoles were likely from a single egg clutch.

On 9 July 2023, we observed *Duttaphrynus bengalensis* tadpoles in pools 2 and 3. The tadpoles were now ~stage 30–35, and for some individuals it was possible to see fine, golden iridocytes across their black dorsal surface (Leong & Chou, 1999). On 16 July 2023, we observed *Duttaphrynus bengalensis* tadpoles (now ~stage 35–40) in pools 2, 3, 4, 5 and 6 but not in pools 7 or 8. On both 9 July and 16 July 2023, most tadpoles were distributed around pool edges out of the main water current and were feeding on algae or substrate or were stationary (Fig. 2).

We did not observe tadpoles of any other anuran species on 2–16 July 2023, nor did we observe metamorphs of any anuran species during this period. However, on 20 July 2023, in addition to observing many ~stage 35–41 *Duttaphrynus bengalensis* tadpoles in pools 2–6, we saw 12 *Duttaphrynus bengalensis* metamorphs ~10 mm snout-urostyle length at pool 3 (Fig. 3). These metamorph toads had completely resorbed their tails and were actively hopping on rocks or grass up to 1 m from the waters' edge. For the related bufonid *Rhinella marina* which has similar sized tadpoles and metamorphs, full tail resorption takes 2–3 days after tadpoles reach stage 42 (the stage at which all four limbs have emerged from the tadpole body but the tail is still well developed; MRC, pers. obs.). Given that the most developed *Duttaphrynus bengalensis* tadpoles we saw on 16 July 2023 were stage 40, the earliest date these tadpoles could have reached stage 42 would be the following day (17 July 2023). Therefore, we estimate the *Duttaphrynus bengalensis* metamorphs we observed on 20 July 2023 completed tail resorption and were fully metamorphosed 2–3 days after 17 July 2023 (i.e., completed metamorphosis on 19–20 July 2023).

Based on published data for egg and hatchling development times for the *Duttaphrynus melanostictus* complex, and unpublished data for development times of early-stage *Rhinella marina* tadpoles (MRC, pers. obs.), we estimate the stage 26–27 *Duttaphrynus bengalensis* tadpoles we observed in pool 2 on 2 July 2023 were 7–10 days old since egg deposition, 6–8 days old since emerging from the egg string as hatchlings and 2–3 days old since transitioning from hatchlings into stage 25 tadpoles (Table 1). Combining these estimates with our estimate that the metamorphs we observed on 20 July

2023 likely completed metamorphosis on 19–20 July 2023, we conclude that the development times for *Duttaphrynus bengalensis* were: egg deposition to metamorphosis 24–28 days, hatchling to metamorphosis 23–26 days and stage 25 tadpole to metamorphosis 19–21 days (Table 1).

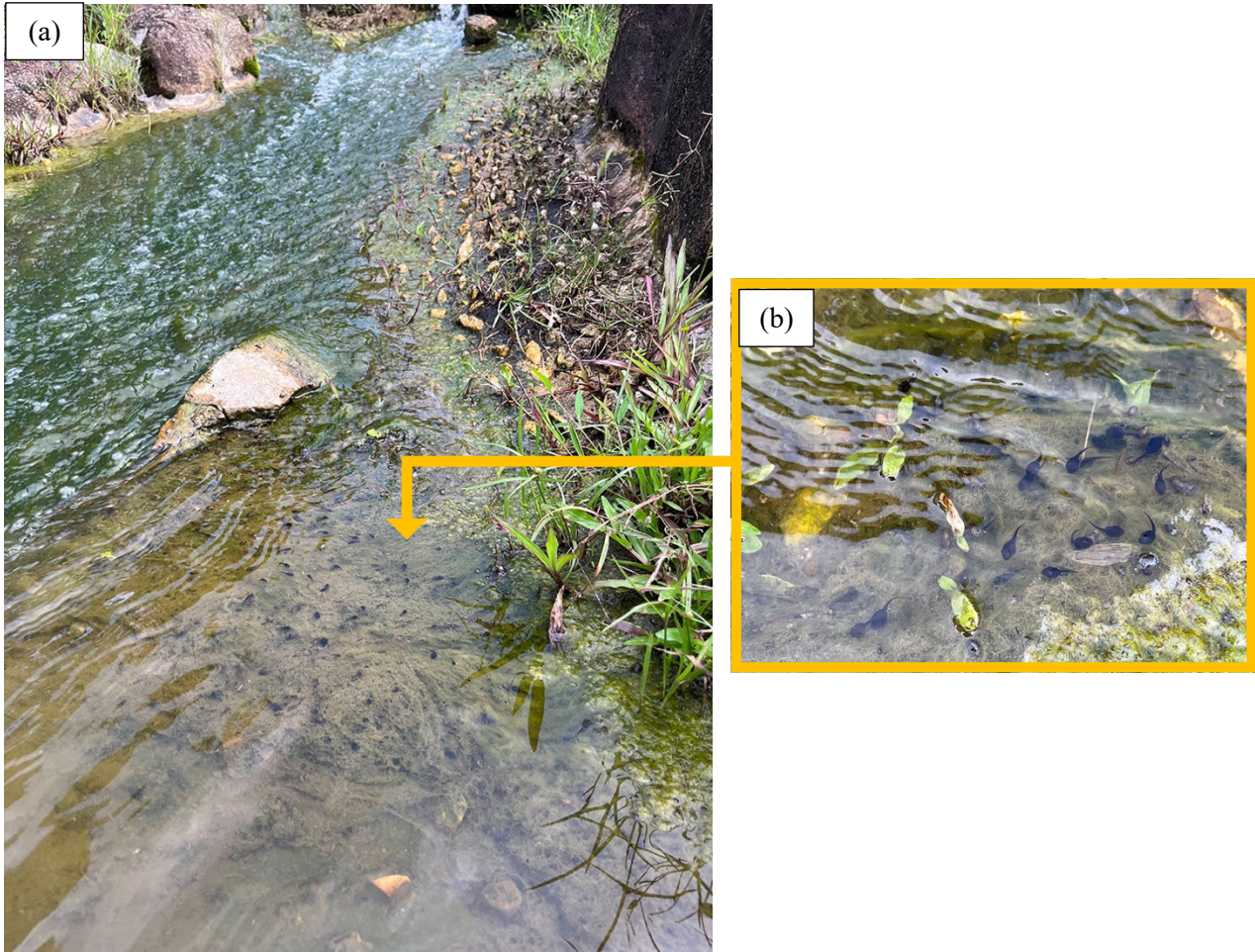


Fig. 2. *Duttaphrynus bengalensis* tadpoles. (a), Arrow indicates position of tadpoles (black objects) out of the main water current. (b), Close-up of tadpoles in Fig. 2a. (Photographs by M. R. Crossland and S. F. Chan).

During each daytime visit to the wetland, we observed several species of potential tadpole predators. Fishing spiders were always present at the water's edge at pools 2, 3 and 4. In pools 7 and 8, we always saw red-eared slider turtles (*Trachemys scripta elegans*, non-native) and several fish species including common snakehead (*Channa striata*, native), silver arowana (*Osteoglossum bicirrhosum*, non-native), common carp or koi (*Cyprinus carpio*, non-native) and redhead cichlid (*Veija melanura*, non-native). We never saw fish or turtles in pools 1–6.

The only anuran species we observed at the wetland at night was *Duttaphrynus bengalensis* (two sub-adults, three adult males, three adult females; Fig. 3).

DISCUSSION

Our estimates of time to metamorphosis for *Duttaphrynus bengalensis* in an urban wetland (24–28 days from egg deposition to metamorphosis, 23–26 days from hatchling to metamorphosis and 19–21 days from stage 25 tadpole to metamorphosis) are comparable to previous (albeit not explicitly defined) estimates for *Duttaphrynus melanostictus* in nature in India (18–20 days: Mahapatra et al., 2017; 25–30 days: Saidapur & Girish, 2001). Similarly, Köhler & Thammachoti (2023) found that, when raised in plastic containers at ambient room temperature of 26–33°C (total daily range) with regular feeding and water changes, *Duttaphrynus melanostictus* tadpoles in Thailand can complete metamorphosis 21 days after egg deposition. Overall, these results demonstrate the capacity of tadpoles of the *Duttaphrynus melanostictus* complex to develop rapidly, which allows the effective use of temporary waterbodies as breeding sites. Bufonid species in general may be capable of rapid aquatic development in warm environments. For example, in northern Australia, the cane toad *Rhinella marina* can complete development from egg deposition to metamorphosis in 16 days when eggs are laid in shallow, hot ephemeral waterbodies (MRC, pers. obs.). Similarly, Chandramouli & Kalaimani (2014) reported that tadpoles of Günther's toad *Duttaphrynus hololius* in small, natural puddles develop from stage 27 to stage 43 (i.e., to metamorphosis; Gosner, 1960) in 7 days.

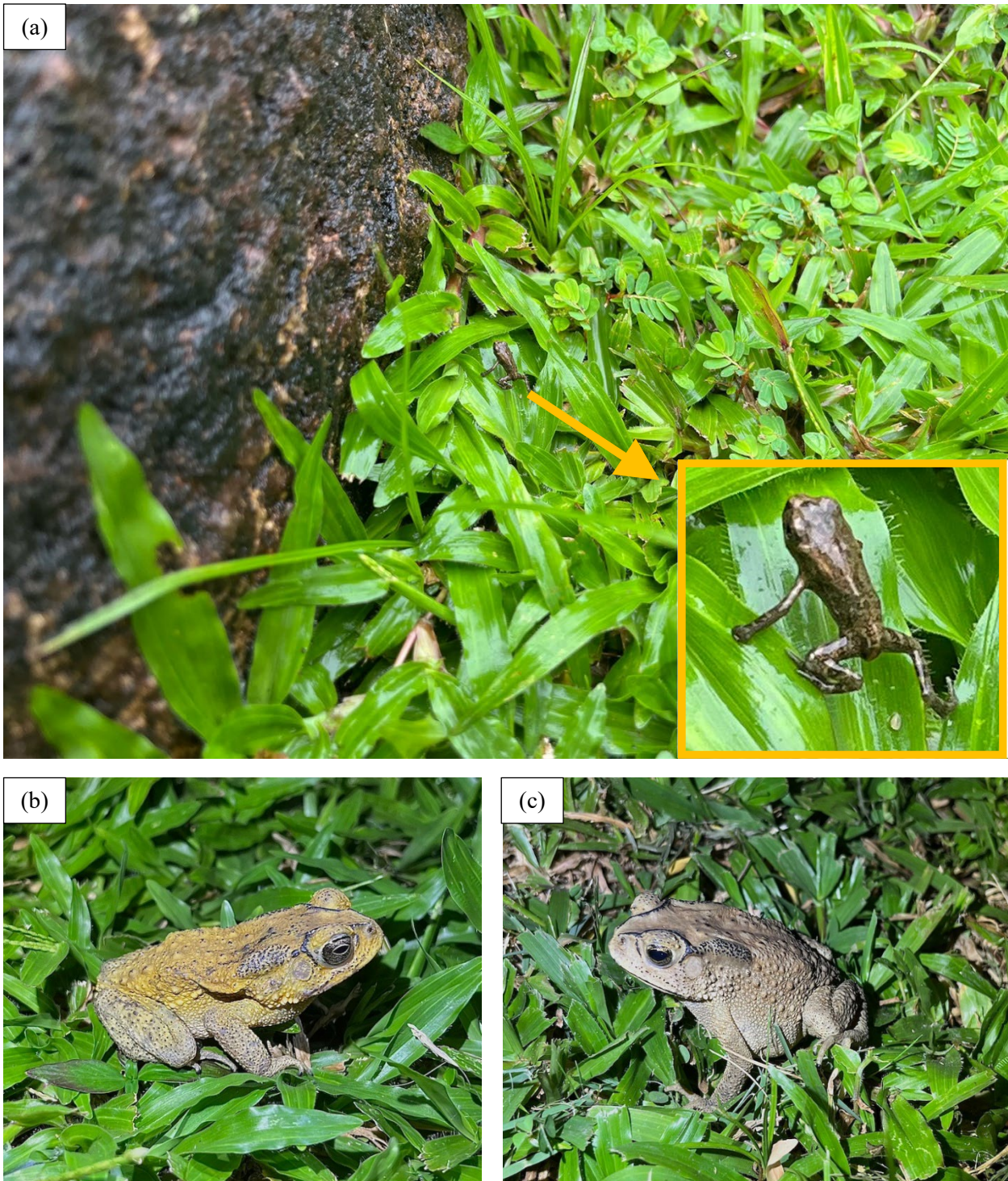


Fig. 3. *Duttaphrynus bengalensis* observed at the wetland. (a), Metamorph (inset is close-up). (b), Adult male. (c), Adult female. (Photographs by M. R. Crossland and S. F. Chan).

Each time we visited the wetland, we observed that *Duttaphrynus bengalensis* tadpoles were present in ever-increasing numbers of pools downstream of our first observations in pool 2. We do not believe this is an artefact of us failing to observe tadpoles in these downstream pools on our first visit on 2 July 2023 because pools 1–5 were very small and shallow with excellent water clarity, while pool 6 had very good water clarity within 1 m of the edge (a microhabitat where one would expect to see toad eggs, hatchlings or tadpoles). Therefore, based on the similarity in tadpole size and development stage among multiple pools on 9 July 2023 and again on 16 July 2023, we suspect that the larger and more developed tadpoles we observed in the lower pools on these dates had likely dispersed and/or been displaced downstream from pool 2 after 2 July 2023. This could have easily occurred because pools 2–6 were connected by shallow riffles and runs. In addition, the general region received 40.0 mm rainfall between 2–9 July 2023 (including 29.6 mm in one 24-hour period), and 49.8 mm rainfall between 9–16 July 2023 (including 25.6 mm in one 24-hour period). This rain, especially during the highest rainfall days, may have contributed to the downstream displacement of tadpoles after 2 July 2023.

Table 1. Calculations for time to metamorphosis for *Duttaphrynus bengalensis* tadpoles observed in a small urban wetland in Singapore, July 2023. Tadpole stages refer to Gosner (1960). Stage 26–27 tadpoles were observed in pool 2 of the wetland on 2 July 2023, and fully metamorphosed individuals were first observed on 20 July 2023. Metamorphosis is defined as emergence of fore- and hindlimbs, and complete resorption of tail. Published references refer to embryonic development of populations of the *Duttaphrynus melanostictus* complex outside Singapore.

Development Period	Minimum Number of Days	Maximum Number of Days	References and Notes
Egg to hatchling	1	1.5	Fan et al., 2016; Saidapur & Girish, 2000, 2001; Kelly et al., 2023
Hatchling to stage 25 tadpole	4	5	Saidapur & Girish, 2000; Karraker, 2011; Jayawardena et al., 2017
Stage 25 tadpole to stage 26–27 tadpole	2	3	Estimate based on <i>Rhinella marina</i> tadpoles (MRC, unpublished data)
Stage 26–27 tadpole to metamorphosis	17	18	Based on current observations; Stage 26–27 tadpoles observed on 2 July 2023; Metamorphosis estimated to have completed on 19–20 July 2023 (see text for details)
Estimated Total Development Time			
Egg to metamorphosis	24	27.5	
Hatchling to metamorphosis	23	26	
Stage 25 tadpole to metamorphosis	19	21	

We found that *Duttaphrynus bengalensis* tadpoles were ultimately present in pools 2–6, but we did not observe any tadpoles in pools 7 and 8 on any visits to the wetland. These lower two pools had the highest turbidity which would have reduced the chances of seeing tadpoles. However, water clarity within 0.5–1 m of the edge of these pools was sufficiently good that we could see through the water column to the substrate, so we would have been able to see any *Duttaphrynus bengalensis* tadpoles present near the pool edge. Additionally, we should have seen any *Duttaphrynus bengalensis* tadpoles swimming further offshore at the water surface due to their conspicuous black colour, despite high water turbidity; such observations are frequently made for similarly sized black *Rhinella marina* tadpoles in highly turbid waterbodies in northern Australia (MRC, pers. obs.).

The apparent absence of *Duttaphrynus bengalensis* tadpoles in pools 7 and 8 might indicate that tadpoles never entered these pools. Alternately, tadpoles may have been washed into these pools but did not survive because they were damaged while passing through the small waterfalls that fed into these pools. We did not observe any tadpole carcasses in pools 7 and 8, although these would likely degrade quickly in a tropical wetland. Another possibility is that tadpoles did survive being washed into pools 7 and 8 but were subsequently eaten by the vertebrate predators (turtles, fish) that are present in these pools but are absent from pools 2–6. This might seem unlikely because, like other bufonid species, tadpoles of the *Duttaphrynus melanostictus* complex (as well as eggs and hatchlings) contain chemicals that are unpalatable or toxic (Keomany et al., 2007; Bickford et al., 2010; Karraker, 2011; Fan et al., 2016; Fan & Lin, 2017). However, such defences might not be absolute. For example, in Australia the early developmental stage tadpoles of the introduced cane toad (*Rhinella marina*) are highly toxic to some native aquatic predators (i.e., lethal if ingested) but are consumed by native turtles without any apparent ill effect (Crossland & Alford, 1998). Additionally, the toxicity of *Duttaphrynus melanostictus* tadpoles is presumed to significantly decline close to metamorphosis (Kelly et al., 2023). If this is true, late-stage *Duttaphrynus bengalensis* tadpoles might be consumed by some aquatic predators without ill effect.

During our observations, the behaviour of *Duttaphrynus bengalensis* tadpoles was either resting or grazing on algae and substrate. We did not observe any aggressive interactions among tadpoles. In contrast, Mahapatra et al. (2017) observed that *Duttaphrynus melanostictus* tadpoles in natural ponds in India were cannibalistic on conspecific eggs, tadpoles and metamorphosing individuals. The observations of Mahapatra et al. (2017) were made when a desiccating temporary pool became divided into multiple small pools, resulting in tadpoles occurring in significantly increased densities. In contrast, the tadpoles we observed were in permanent flowing water at relatively low densities with apparently abundant food. Thus, cannibalism in this species complex may be a plastic behavioural trait triggered by stressful environmental conditions that did not occur in the wetland we visited (e.g., Jefferson et al., 2014).

In summary, our observations add to the knowledge of the natural history of *Duttaphrynus bengalensis* and demonstrate the successful breeding of this toad in a small urban wetland. Such environments are common in Singapore, and therefore likely play an important role in the persistence of the non-native population of *Duttaphrynus bengalensis* in this highly urbanised city-state.

ACKNOWLEDGEMENTS

We are grateful to Heok Hui Tan and Kelvin Lim from the Lee Kong Chian Natural History Museum, National University of Singapore for identifying freshwater fish based on photographs we took at the wetland, and for providing access to scientific articles, respectively. We also thank an anonymous reviewer who made very helpful suggestions to an earlier draft of this paper.

LITERATURE CITED

- Alford RA (1999) Ecology: Resource use, competition, and predation. In: McDiarmid RW & Altig R (eds.) Tadpoles: The Biology of Anuran Larvae. University of Chicago Press, Chicago, pp. 240–278.
- Baker N & Lim KKP (2012) Wild Animals of Singapore: A Photographic Guide to Mammals, Reptiles, Amphibians and Freshwater Fishes. Updated edition. Draco Publishing and Distribution Pte. Ltd. and Nature Society (Singapore), Singapore, 180 pp.
- Berry PY (1964) The breeding patterns of seven species of Singapore Anura. *Journal of Animal Ecology*, 33: 227–243.
- Bickford D, Ng TH, Qie L, Kudavidanage EP & Bradshaw CJA (2010) Forest fragmentation and breeding habitat characteristics explain frog diversity and abundance in Singapore. *Biotropica*, 42: 119–125.
- Chan SH & Goh C (2010) Frogs of Sungei Buloh Wetland Reserve (Amphibia: Anura). *Nature in Singapore*, 3: 103–116.
- Chandramouli SR & Kalaimani A (2014) Description of the larvae of Günther's toad *Duttaphrynus hololius* (Günther, 1876) (Anura: Bufonidae) with notes on development and oral structure. *Alytes*, 31: 3–12.
- Crossland MR & Alford RA (1998) Evaluation of the toxicity of eggs, hatchlings and tadpoles of the introduced toad *Bufo marinus* (Anura: Bufonidae) to native Australian aquatic predators. *Australian Journal of Ecology*, 23: 129–137.
- Fan XL & Lin ZH (2017) Vulnerability and behavioral responses of South Chinese anuran tadpoles to native dragonfly (*Pantala flavescens*) naiads and introduced western mosquitofish (*Gambusia affinis*). *Journal of Freshwater Ecology*, 32: 529–539.
- Fan X, Lin Z, Li X, Wei L & Ding G (2016) Effects of predation by invasive western mosquitofish (*Gambusia affinis*) on survival of eggs, embryos and tadpoles of *Pelophylax nigromaculatus* and *Duttaphrynus melanostictus* in South China. *Asian Herpetological Research*, 7: 46–52.
- Figuroa A, Low MEY & Lim KKP (2023) Singapore's herpetofauna: updated and annotated checklist, history, conservation, and distribution. *Zootaxa*, 5287: 1–378.
- Gosner KL (1960) A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, 16: 183–190.
- Gramapurohit NP & Radder RS (2012) Mating pattern, spawning behaviour, and sexual size dimorphism in the tropical toad *Bufo melanostictus* (Schn.). *Journal of Herpetology*, 46: 412–416.
- Jablonski D, Masroor R & Hofmann S (2022) On the edge of the Shivaliks: An insight into the origin and taxonomic position of Pakistani toads from the *Duttaphrynus melanostictus* complex (Amphibia, Bufonidae). *Zoosystematics and Evolution*, 98: 275–284.
- Jayawardena UA, Rohr JR, Amerasinghe PH, Navaratne AN & Rajakaruna RS (2017) Effects of agrochemicals on disease severity of *Acanthostomum burminis* infections (Digenea: Trematoda) in the Asian common toad, *Duttaphrynus melanostictus*. *BMC Zoology*, 2: 13.
- Jefferson DM, Hobson KA & Chivers DP (2014) Time to feed: How diet, competition, and experience may influence feeding behaviour and cannibalism in wood frog tadpoles *Lithobates sylvaticus*. *Current Zoology*, 60: 571–580.
- Jørgensen B, Shakuntala K & Vijayakumar S (1986) Body size, reproduction and growth in a tropical toad, *Bufo melanostictus*, with a comparison of ovarian cycles in tropical and temperate zone anurans. *Oikos*, 46: 379–389.
- Karraker NE (2011) Are toad tadpoles unpalatable: Evidence from the behaviour of a predatory dragonfly in South China. *Amphibia-Reptilia*, 32: 413–418.
- Kelly CL, Schwarzkopf L, Christy TM & Kennedy MS (2023) The toad less travelled: Comparing life histories, ecological niches, and potential habitat of Asian black-spined toads and cane toads. *Wildlife Research*, 51: WR22111.
- Keomany S, Mayxay M, Souvannasing P, Vilayhong C, Stuart BL, Srour L & Newton PN (2007) Toad poisoning in Laos. *American Journal of Tropical Medicine and Hygiene*, 77: 850–853.
- Köhler G & Thammachoti P (2023) Comparative study of the larval development of four anuran species from the Khorat Plateau, Thailand. *Raffles Bulletin of Zoology*, 71: 26–50.
- Leong TM & Chou LM (1999) Larval diversity and development in the Singapore Anura (Amphibia). *The Raffles Bulletin of Zoology*, 47: 81–137.
- Licata F, Andreone F, Freeman K, Rabesianaka S, Robsomanitrndrasana E, Reardon JT & Crottini A (2020) The Asian toad (*Duttaphrynus melanostictus*) in Madagascar: A report of an ongoing invasion. In: Angelici FM & Rossi L (eds.) *Problematic Wildlife II*. Springer, Switzerland, pp. 617–638.
- Mahapatra S, Dutta S & Sahoo G (2017) Opportunistic predatory behaviour in *Duttaphrynus melanostictus* (Schneider, 1799) tadpoles. *Current Science*, 112: 1755–1759.
- Mogali S, Saidapur S & Shanbhag B (2017) Influence of desiccation threat on the metamorphic traits of the Asian common toad, *Duttaphrynus melanostictus* (Anura). *Acta Herpetologica*, 12: 175–180.

- Ngo BV & Ngo CD (2013) Reproductive activity and advertisement calls of the Asian common toad *Duttaphrynus melanostictus* (Amphibia, Anura, Bufonidae) from Bach Ma National Park, Vietnam. *Zoological Studies*, 52: 12.
- O'Shea M, Sanchez C, Kathriner A, Mecke S, Lopez Carvalho V, Varela Ribeiro A, Afranio Soares Z, Lemos de Araujo L & Kaiser H (2015) Herpetological diversity of Timor-Leste: Updates and a review of species distributions. *Asian Herpetological Research*, 6: 73–131.
- Othman SN, Chen YH, Chuang MF, Andersen D, Jang Y & Borzée A (2020) Impact of the mid-Pleistocene revolution and anthropogenic factors on the dispersion of Asian black-spined toads (*Duttaphrynus melanostictus*). *Animals*, 10: 1157.
- Saidapur SK & Girish S (2000) The ontogeny of kin recognition in tadpoles of the toad *Bufo melanostictus* (Anura: Bufonidae). *Journal of Biosciences*, 25: 267–273.
- Saidapur SK & Girish S (2001) Growth and metamorphosis of *Bufo melanostictus* tadpoles: Effects of kinship and density. *Journal of Herpetology*, 35: 249–254.
- Schneider CA, Rasband WS & Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9: 671–675.
- Soorae PS, Frankham GJ & Mohamed AA (2020) The first record of the Asian common toad *Duttaphrynus melanostictus* Schneider, 1799 in Abu Dhabi, United Arab Emirates. *BioInvasions Records*, 9: 434–443.
- Trainor CR (2009) Survey of a population of black-spined toad *Bufo melanostictus* in Timor-Leste: Confirming identity, distribution, abundance and impacts of an invasive and toxic toad. A Report by Charles Darwin University to AusAID under contract agreement NO. 52294, 48 pp.
- Wogan GOU, Stuart BL, Iskandar DT & McGuire JA (2016) Deep genetic structure and ecological divergence in a widespread human commensal toad. *Biology Letters*, 12: 20150807.