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Paedomorphic Blotched Tiger Salamander (*Ambystoma mavortium melanostictum) in ovo* counts, British Columbia, Canada

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Abstract

Reproductively mature larval morphs, known as paedogens, are a rare occurrence in Blotched Tiger Salamander (*Ambystoma mavortium melanostictum*). The Southern Mountain population of this subspecies, confined to the southern interior of British Columbia, is listed federally as Endangered and has been facing increasing pressures from anthropogenic stressors in both their aquatic and terrestrial landscapes. In 2017, we examined a subset of 36 frozen Blotched Tiger Salamander paedogens collected in September 1985 after rotenone treatment in preparation for a recreational fishery near Oliver, British Columbia. We estimated total *in ovo* numbers in nine gravid individuals to gain insight into paedogen reproductive condition. The number of eggs per individual averaged 227 ± 109 [SD]; range 28–421), with larger dark eggs accounting for 133 ± 69 and smaller pale eggs (possibly follicles or colour may be an artifact of storage) accounting for 94 ± 49. Salamanders were collected in September after the expected egg-laying period for the terrestrial form (early spring); thus, the reproductive stage of the eggs is unclear, but is assumed to be post-breeding and representative of developing eggs and follicles. Canadian data on *in ovo* counts within the body cavity have not been reported for Blotched Tiger Salamander paedogens and our study provides valuable information on the reproductive condition of paedogens. Although terrestrial forms have been observed, the presence of paedogens in the treated wetland has yet to be detected.

Key words: Blotched Tiger Salamander; *Ambystoma mavortium melanostictum*; egg mass; reproduction; life history; neotene; neoteny; paedogenal metamorphosis

Introduction

Paedomorphism is a developmental process found in some urodele amphibians where metamorphosis is delayed, but a sexually mature aquatic adult that resembles its larval form develops and is referred to as a paedogen (Pierce and Smith 1979). Paedomorphism may be a result of complex environmental cues, resources, and site conditions. The occurrence of paedogens in the Southern Mountain population of Blotched Tiger Salamander (*Ambystoma mavortium melanostictum*) in the Similkameen, Okanagan, and Kettle River Valleys of British Columbia is poorly documented and has only been detected in five wetland locations (COSEWIC 2012). Wetlands in the south Okanagan River Valley can have coexisting terrestrial and aquatic breeding forms (S.L.A. pers. obs.; also observed in Mole Salamander [*Ambystoma talpoideum*] by Semlitsch 1985) and the species is generally observed in fishless wetlands (COSEWIC 2012). Historically, wetlands throughout the upper and lower benches of the south Okanagan were most likely all fishless (J. Mitchell pers. comm. 2008). Salamanders and fish do coexist in a few locations in the south Okanagan, for unknown reasons, although habitat complexity may play a role (Ashpole 2015).

The Southern Mountain population of Blotched Tiger Salamander, a subspecies of Western Tiger Salamander (*Ambystoma mavortium*), is listed federally as Endangered in Canada and restricted to British Columbia (ECCC 2017). Similar to other amphibian species, Blotched Tiger Salamanders experience a variety of anthropogenic pressures, including habitat degradation, fragmentation and isolation, agricultural contaminants, introduced predatory fish species, and increased drought affecting wetland hydrology (ECCC 2017). Because this population is localized at the northern edge of the subspecies' range, its reproductive biology is not completely known and information from southern populations is often presumed (Collins *et al.* 1980; Matsuda *et al*. 2006; IUCN 2015; ECCC 2017). Beyond water body permanence, specific breeding habitat requirements for Blotched Tiger

Salamander paedogens are not clear (COSEWIC 2012). In the terrestrial form, courtship and mating occur after the first heavy rainfall in March or April and cease in May when terrestrial adults return to upland habitats (ECCC 2017). Larvae hatch within three weeks and remain aquatic until early summer (July to August); however, some may overwinter until the following spring (ECCC 2017). The timing of courtship and egg-laying for paedogens is assumed to be similar to that for the terrestrial form.

Disparity of egg mass counts for terrestrial Blotched Tiger Salamander have been reported from American sources, with some research indicating that eggs are singly laid on submerged vegetation (Corkran and Thomas 1996; Collins *et al.* 1980) and others reporting large or variable clusters ranging from 23 eggs (Anderson *et al*. 1971) to 120 eggs (Anderson *et al.* 1971; Corkran and Thomas 1996). The differences in number of eggs per mass laid at one time may be related to the total number of mature eggs present *in ovo* and whether individuals oviposit eggs serially in multiple small clusters or all at once within the season. The only research explicitly examining egg counts from dissected paedogen ovaries reports up to 5670 ± 1021 (SD) per individual (n = 13; Rose and Armentout 1976).

Uncertainty about Blotched Tiger Salamander fecundity is especially true for paedomorphic individuals, whose biology and ecology may be different from that of their terrestrial counterparts. Paedomorphs have been observed mostly in warm, shallow, permanent ponds and lake edges where there is little risk of predation by fish or invasive organisms (Collins *et al*. 1980; Whiteman 1994; Corkran and Thomas 1996; Anderson and Whiteman 2015). The reproductively mature larval form has been observed to occur in other *Ambystoma* salamanders as a result of environmental and interspecific species relations; paedomorphism is theorized to increase fitness under specific environmental conditions (e.g., high resource availability, optimal aquatic habitat; Semlitsch and Wilbur 1989; Denoël *et al*. 2005; Anderson and Whiteman 2015).

Here we record *in ovo* counts from the dissected ovaries of paedogens from the Southern Mountain population of Blotched Tiger Salamanders recovered from a permanent wetland after a rotenone treatment to eradicate Pumpkinseed Sunfish (*Lepomis gibbosus*), Rainbow Trout (*Oncorhynchus mykiss*), and Small-mouth Bass (*Micropterus dolomieu*) in preparation for a trout fishery.

Methods

Dead adult Blotched Tiger Salamanders were collected after a rotenone treatment in September 1986 near Oliver, British Columbia (49.1823°N, 119.5504°W; Ministry of Environment 1986). In total, 176 salamanders were collected (19 unknown sex presumed juvenile, 92 females, 65 males). Although the species was validated and notes on sex based on gross morphology were made by experienced local herpetologists, it is unclear from the records if all collected individuals were paedogens. A subsample of 36 frozen (–18°C) paedogens was retained and re-examined in 2014, necropsied, measured, stomach contents macroscopically inspected, and sexed using gross morphology (presence of oviducts and/or eggs or testis). It is not clear why this particular subset of 36 specimens was retained and the subset may represent a biased sampling of individuals from the population. Whole sunfish were detected in the oral cavity or stomach contents of seven salamanders. A subsample of 11 females was subsequently placed in individual specimen jars filled with ethanol and stored. The subsample was selected based on well-preserved intact specimens; decayed or damaged individuals were discarded. In 2017, eggs were removed from each individual and counted using a stereomicroscope (16× magnification; Zeiss Stemi, Model 3919021628, Jena, Germany). To ensure accuracy during egg counts, S.L.A. and M.R.N. conducted independent (blind) counts of each mass and recorded total number of eggs, eggs that appeared notably smaller or paler, and larger dark eggs (Figure 1).

Results

The 176 adult specimens collected were female biased, with a ratio of 1.4 females to every male, assuming sexing was accurate. From the more closely

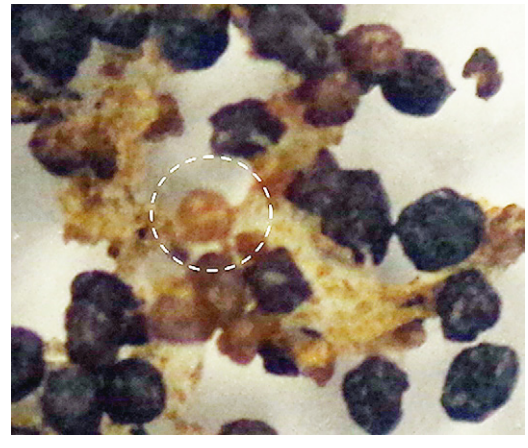

Figure 1. Eggs of a paedomorphic Blotched Tiger Salamander (*Ambystoma mavortium melanostictum*) from near Oliver, British Columbia, Canada, observed through a stereomicroscope (16×). Eggs were either smaller, pale, immature (white circle) or larger, dark, mature. Photo: S. Ashpole.

examined subsample of 36 specimens, 17 were of unknown sex (presumed immature; mean total length [TL] ± SD 12.0 ± 1.0 cm; range 9.8–13.6 cm), five were male (TL 14.3 ± 1.6 cm; range 13.8–17.5 cm), and three were non-gravid females (TL 17.0 ± 0.5 cm; range 16.3–17.3 cm). The remaining 11 specimens were gravid females and the largest of the subsample (TL 18.0 ± 1.7 cm; range 16.2–22.0 cm). Two of the latter were omitted from egg counts because of decomposed egg tissue.

Egg masses in each of the nine gravid females were found to consist of both smaller (3–6 mm) and larger eggs (7–11 mm), with large eggs 1.5 times bigger than small eggs and darker brown to black in colouration. Immature eggs were smaller, much lighter in colour, and less numerous than mature eggs. The eggs were contained in translucent gelatinous sacs located bilaterally within the individual, ventral to the kidney structures. Number of eggs in each female varied considerably, from 28 to 421 (average 227 ± 109), with larger dark eggs accounting for 133 ± 69 and smaller pale immature-looking eggs accounting for 94 ± 49 per individual. The total number of eggs per female was positively correlated with total body length (r = 0.98; Figure 2). Inter-observer variability was low for total number of eggs (± 4 eggs), but slightly higher for counts of larger dark eggs and smaller pale eggs (± 18 eggs).

Discussion

The number of eggs in an individual paedomorphic Blotched Tiger Salamander (28–421) was considerably smaller than estimates provided in the recovery strategy for the terrestrial form of this species (5000 eggs/mass based on Rose and Armentrout 1976; ECCC 2017). The difference, which was at least one order of magnitude, has substantial conservation implications for protection and management of the species. Our findings are comparable to those of Collins *et al.* (1980), who reported terrestrial forms with 23–110 eggs/mass, although our counts represent total number of eggs in the body cavity versus ovideposited eggs. It is not clear how eggs are deposited by paedogens and whether deposition occurs in a single event or as several clusters over time. Similarly, the developmental cycle of eggs in our species is not documented, but presumed to be similar to the terrestrial form because of the timing of environmental conditions. Previous studies have reported location and distribution of terrestrial *A. mavortium* egg-laying sites within their habitat (Anderson *et al.* 1971; Sever and Dineen 1977; Collins *et al.* 1980; Corkran and Thomas 1996; Ministry of Environment and Climate Change Strategy 2014), but information on paedogens remain undocumented. Egg-laying characteristics may be particularly challenging if eggs of the terrestrial form are indistinguishable from those of the aquatic form.

Similarly, it is not clear whether the reproductive cycle or ecology of Blotched Tiger Salamander paedogens in the southern interior of British Columbia are similar to those of other populations of this subspecies in British Columbia or other morphs, throughout the subspecies' range. Rose and Armentout (1976) report discontinuities of gene flow in western subspecies of tiger salamanders, leading to significantly

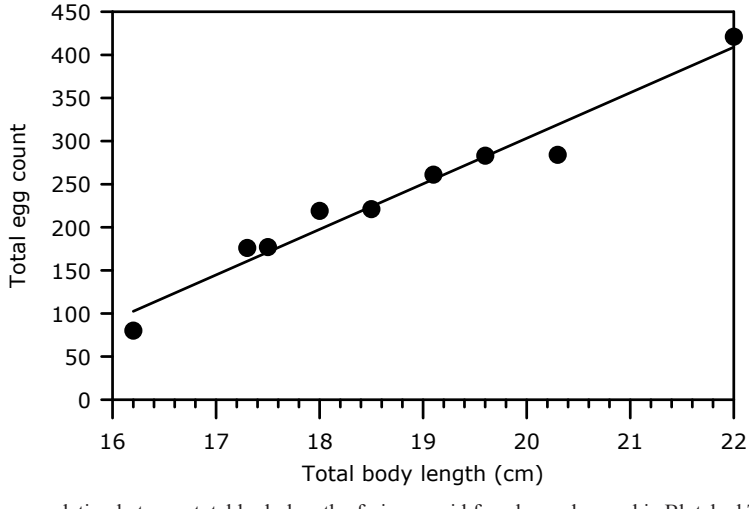

Figure 2. Positive correlation between total body length of nine gravid female paedomorphic Blotched Tiger Salamanders (*Ambystoma mavortium melanostictum*) from near Oliver, British Columbia, with total egg count (Pearson product-moment correlation coefficient, r = 0.98).

variable metamorphic rates, size limits, and some physiological parameters. Female paedogens in our population ranged from 17.0 to 22.0 cm TL, whereas the largest females reported by Rose and Armentout (1976) from New Mexico were smaller at 14.3 cm (range 13.9–14.7 cm). California Tiger Salamander (*Ambystoma californiense*) males averaged 20.1 cm and females averaged 16.8 cm in TL, with sex ratios varying from 0.8:1 (1992) to 8.1:1 (1993; Loredo and Van Vuren 1996). The variability suggests that information gleaned from our study should remain within the south Okanagan context.

As paedogens occur in permanent aquatic habitat, it is also possible that the conversion of wetlands in the southern interior to ephemeral, human-made ponds (Lea 2008) may lead to smaller populations of the paedogenic form because of lack of suitable habitat throughout the area. More investigation into the reproductive biology and behaviour of Blotched Tiger Salamander, in all forms, is required to accurately elucidate the reproductive potential of this species and inform recovery efforts and conservation of wetlands. For this particular site, terrestrial salamanders have been observed, but paedogens have not been detected since the rotenone treatment. Confirmation of the continued presence or re-establishment of tiger salamander paedogens will require more intensive surveying. Further examination of the persistent effects of rotenone applications on these important permanent wetland habitats is critical for conservation of amphibian species as recreational fish management continues. Finally, we are still uncertain how such a large number of paedomorphic salamanders survived and were subsequently salvaged from a wetland in the presence of introduced predatory fish. Sunfish and bass species are known predators of amphibian larvae (Riley *et al.* 2003; Preston *et al.* 2012) and are thought to have a severe impact on amphibian larvae. It is often assumed that paedomorphic salamanders are excluded from sites with predatory fish (Sprules 1974; COSEWIC 2012).

Author Contributions

Writing – Original Draft: M.R.N.; Writing – Review & Editing: S.L.A.; Conceptualization: S.L.A.; Investigation: M.R.N. and S.L.A.; Methodology: S.L.A.; Formal Analysis: M.R.N. and S.L.A.; Funding Acquisition: S.L.A.

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