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Article in *Northwestern Naturalist* · February 2010

DOI: 10.1898/NWN09-23.1

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FIELD OBSERVATIONS OF OVIPOSITION AND EARLY DEVELOPMENT OF THE COASTAL TAILED FROG (*ASCAPHUS TRUEI*)

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Key words: *Ascaphus truei*, clutch size, Coastal Tailed Frog, communal oviposition, early development, growth, Olympic Peninsula, Washington State

Tailed frogs (genus *Ascaphus*) are stream amphibians endemic to the Pacific Northwest (Jones and others 2005) that are thought to represent the sister taxon of all other living anurans (Ford and Cannatella 1993; Haas 2003). Among their unique characteristics is their reproductive mode. Of the 5912 described anuran species (AmphibiaWeb 2010), the 2 species of tailed frog are the only anurans known to engage in copulation that includes intromission (Sever and others 2001). Further, the sperm storage capability of females allows temporal separation between breeding and oviposition, resulting in females depositing eggs alone (Metter 1964; Brown 1989).

Knowledge of tailed frog oviposition sites, which are always concealed in streambeds, is limited (Karraker and others 2006 and references therein). What is known is based on the opportunistic discovery of sites during the examination of instream substrates, a standard procedure of various types of stream surveys (for example, Adams 1993; Bury and others 2001). These haphazard discoveries have resulted in encountering various stages of clutch development, but have never involved field observation of oviposition. Observations of development from oviposition also have been restricted to females laying eggs in a laboratory via hormonal induction (Wernz and Storm 1969; Brown 1975). Here we report the 1st field observation of oviposition by tailed frogs, and selected field data on early development.

Study Area

Our observations were made on Miller Creek (UTM Zone 10, 488225E, 5253553W, WGS84;

elevation approximately 216 m), a 3rd-order non-fish-bearing stream on the east side of the Olympic Peninsula near Lake Cushman, Mason County, Washington. The site of our observations consisted of a long riffle with steady fast-moving water. A bedrock step-pool was located 5.5 m upstream and a small braided cascade was located 5.9 m downstream of the site. Bedrock outcroppings lined the banks up- and downstream for at least 40 m. Surrounding uplands are managed for timber production by the Washington Department of Natural Resources; the local stand was last harvested in 1945. Red Alder (*Alnus rubra*) and Vine Maple (*Acer circinatum*) dominate the riparian overstory; understory is mostly Salmonberry (*Rubus spectabilis*), Devil's Club (*Oplopanax horridus*), and Sword Fern (*Polystichum munitum*). Steep hillslopes (50–65%) are blanketed with 2nd-growth Douglas-fir (*Pseudotsuga menziesii*), Western Hemlock (*Tsuga heterophylla*), and Western Redcedar (*Thuja plicata*). Lithology is mostly Pleistocene age glacial till with large-clast material contributed from the basalt-based Crescent Formation upstream.

Initial Observations of Oviposition

On 29 July 2008, during rubble-rouse sampling (Quinn and others 2007) of a 2-m unit for stream-associated amphibians within this reach, we rolled a large (65 × 60 × 44 cm) boulder that was imbedded about 10 cm in surrounding gravel and sand. Four adult female *A. truei* and at least 183 *A. truei* eggs were found beneath this boulder (Fig. 1). One female was actively laying eggs. A spot water temperature taken at this site at about 11:00 was 12.0°C. A separate group of 24 eggs was found beneath a 2nd boulder (55 × 40 × 24 cm) <1 m downstream that was imbedded in approximately 20 cm of

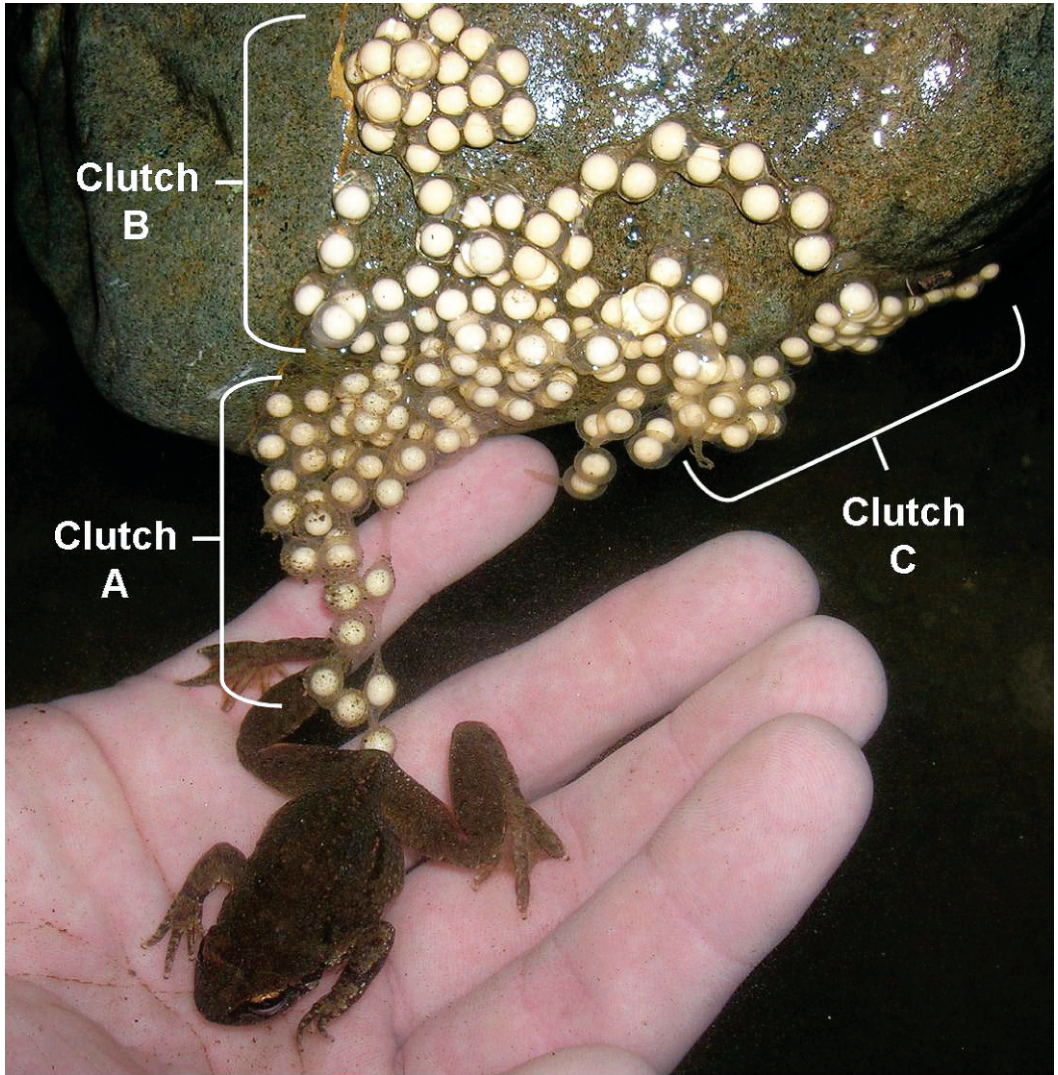


FIGURE 1. Distribution of 183 *A. truei* eggs on the exposed inferior but submerged surface of the oviposition boulder, 29 July 2008. The female *A. truei* laying Clutch A is in the lower foreground. Clutch B consists of paler larger eggs in the central upper portion of the figure. Clutch C consists of the smaller eggs to the right of center on the less visible surface of the boulder.

gravel and sand. A 5th adult female *A. truei* was found <1 m from these eggs. Later examination of photographs of these eggs at 10–15 \times magnification allowed us to estimate clutch size based on egg size, development and distribution, and identify jelly strand connections and termini. We also used the degree of fine debris accumulation on egg surfaces of egg capsules to help distinguish between different clutches. Over our 71-d period of observation, we obtained water

temperatures from a datalogger recording every 0.5 h located 11 m downstream of the 183-egg oviposition site.

We estimated the group of at least 183 eggs to comprise 3 clutches. The female depositing eggs was associated with 68 eggs (hereafter Clutch A; Fig. 1). During handling of this female, 5 eggs still attached to the female broke off the oviposition strands. This female also extruded 2 eggs into the plastic bag in which she was

temporarily placed during handling, so the minimum size of her clutch was 70. The 7 detached eggs were cream-colored with mean ovum and capsular diameters of 4.0 mm and 6.0 mm, respectively. The ovipositing female was 40.0 mm snout-vent length (SVL) with a mass of 7.7 g (taken with the 2 eggs still attached); the 3 non-ovipositing females (40.9 mm SVL, 5.9 g; 37.3 mm SVL, 4.7 g; and 39.5 mm SVL, 5.7 g) had visibly deflated abdomens. We interpreted remaining eggs to represent clutches of 68 and 47 (hereafter Clutches B and C, respectively; Fig. 1). After these initial observations, we replaced the detached eggs and the 4 females beneath the oviposition boulder when it was returned to its original position.

We interpreted the separate group of 24 eggs found beneath the 2nd boulder to constitute a 4th clutch (hereafter Clutch D). These eggs appeared slightly more advanced in development than those in the other 3 clutches. These eggs were beige in color and had ovum and capsular diameters, based on measurement of 4 or 5 eggs and estimation of capsular diameters from photographs, of approximately 4.5 mm and 5.0 mm, respectively. The 5th adult female found near this clutch was 41.5 mm SVL, weighed 7.0 g, and was gravid.

During surveys the following day, we captured 2 additional adult females 124 m downstream from the Clutch A site. One was gravid (41.9 mm SVL, 6.6 g) and the other had a visibly deflated abdomen (39.7 mm SVL, 4.9 g). Based on size, only the female with the visibly deflated abdomen had any likelihood of being one of the same females observed the previous day.

Revisit Observations and Measurements

We revisited the Clutch A site on 12 August 2008. AFP also revisited the Clutch A site and enclosure on 27 August; 8, 15, and 23 September; and 1 and 8 October 2008. Prior to rolling the oviposition boulder during the 12 August revisit, we placed fine-mesh (1.25 × 1.90 mm) soft nylon screening across the stream to intercept unattached eggs that might move downstream. After rolling the boulder, we intercepted 7 loose eggs that we presume originated from Clutch A and placed them in an enclosure containing a rocky matrix simulating streambed conditions. The enclosure was

a 50 × 37 × 16 cm plastic box placed close to the oviposition site. This enclosure had screened ends and feeder pipes to maintain stream flow, and an open top to help approximate ambient environmental conditions.

At each revisit, remaining eggs or larvae hatched from the original eggs in the enclosure were measured (SVL, total length [TL], and mass) and observations were recorded. Where appropriate, data collected during these revisits are presented as the mean ± standard deviation and ranges. We provide only means for cohort growth data because animals were not individually marked. For larval growth, we assessed the fit of regression models for both SVL and TL on time, and describe the data only for the SVL and TL model that was both simplest and had the most explanatory power; that is, had the fewest terms and largest coefficient of determination (r^2).

On 12 August, embryos from Clutch A had developed to the muscular response stage (stage 18; Brown 1989), and averaged 7 and 4 mm in capsular and yolk diameter, respectively (Fig. 2). Over the 2-wk interval from oviposition to 12 August, water temperatures averaged 12.9 ± 0.7°C (range: 11.6 to 14.7°C).

By 27 August, all individuals had hatched. Enclosure hatchlings were translucent white and lacked pigmentation except for their eyes. The 6 enclosure hatchlings we measured (the 7th hatchling was not detected during this visit) were <0.1 g, and averaged 16.9 ± 1.2 mm TL and 6.8 ± 0.4 mm SVL. Five of the 6 had a large amount of yolk (5.1 ± 1.4 mm mean yolk dia), but the 6th hatchling (not included in the yolk average) had abnormal yolk. Water temperatures averaged 13.4 ± 0.9°C (range: 11.6 to 16.0°C) from the date of oviposition of Clutch A to when all embryos were observed to have hatched.

On 8 September, the 7 enclosed larvae averaged 21.2 ± 0.7 mm TL and 7.6 ± 0.2 mm SVL, were all about 0.1 g, and still lacked pigmentation except for their eyes. On 15 September, 1 enclosed larva was beginning to develop the darker pigmentation typical of older larvae; it was mottled with a black band a few millimeters thick that offset a cream-colored tail tip. The other 6 larvae showed this pigmentation pattern on the 23 September revisit. On 1 October, all 7 enclosed larvae



FIGURE 2. Close-up of a portion of *A. truei* Clutch A in muscular response stage (based on Brown 1989), 12 August 2008.

averaged 25.3 ± 0.9 mm TL and 8.6 ± 0.3 mm SVL, and were all about 0.2 g. Over the 35 d of our post-hatching observations (27 August to 1 October), larvae grew an average of 8.4 mm in TL and 1.8 mm in SVL, with TL increasing faster than SVL (Fig. 3). Water temperatures averaged $12.4 \pm 0.7^\circ\text{C}$ (range: 10.8 to 14.7°C). High water overtopped the enclosure presumably allowing all larvae to escape prior to our last revisit on 8 October.

Quadratic regression models were both simplest and best-fitting for both SVL and TL (Fig. 3). Linear, logarithmic, and power models all had a poorer fit for both SVL ($r^2 \leq 0.80$) and TL ($r^2 \leq 0.87$). The third-order model had an equivalent fit for TL ($r^2 = 0.90$) and was incrementally better for SVL ($r^2 = 0.87$), but the added term detracted from model simplicity.

General Comments

The oviposition sites we discovered are similar to sites previously described: a concealed instream location beneath cobbles or boulders (Karraker and others 2006 and references therein). Karraker and others (2006) suggested that oviposition beneath larger rocks may help protect developing embryos from damage during substrate mobility or scour. However, the adhesive strings of tailed frog eggs may tend to constrain placement to single rocks, especially if some kind of substrate preparation behavior to aid adhesion is involved. Substrate preparation behavior, recently reported in the Foothill Yellow-legged Frog (*Rana boylei*; Wheeler and others 2003), could apply to a range of species that deposit eggs on rocky substrates in flowing water (Rombough and Hayes 2005).

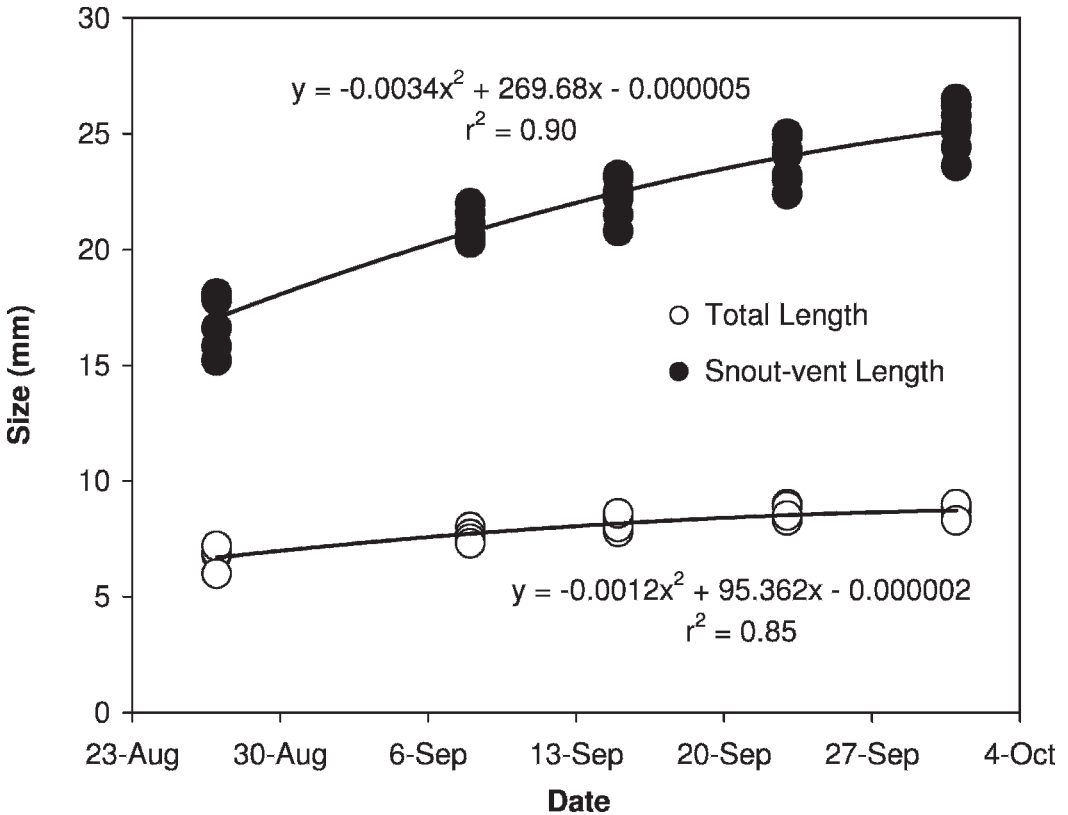


FIGURE 3. Post-hatching growth of larval *A. truei*. The x axis is the timeline in 2008. Except for 27 August when 6 larvae were measured, sample size is 7 for all sample dates. Data are plotted on the day mid-point of each interval from which larval measurements were obtained.

We also recorded communal oviposition, a phenomenon infrequently reported for tailed frogs. Karraker and others (2006) reported that only 4 of 30 (13%) *A. truei* oviposition sites known to them were communal, which they defined as >1 clutch on the same rock. They suggested that the frequency of communal oviposition was underestimated because larger rocks, which would increase the potential opportunity to oviposit communally as they defined it, were less likely to be overturned. It is our opinion, however, that restricting the definition of communal oviposition to what may be laid on a single rock may also compound underestimation of the frequency of this phenomenon. This is particularly true in the context of selected previous studies (for example, Bury and others 2001; D Pilliod and E Hyde in Karraker and others 2006) that involved searches of thousands of tiny (1-m

randomly selected plots that might easily miss communal oviposition that is less restrictively defined.

Reduced predation risk and habitat limitation are additional factors suggested as contributing to communal oviposition in tailed frogs (Karraker and others 2006). The former results in communal oviposition because the likelihood of predation on any 1 clutch may be reduced when clutches are grouped, and the latter because rarity of substrates for oviposition may force grouping. Neither seems a good fit to our observations. Fishes and giant salamanders are thought to be the most important predators on the aquatic life stages of tailed frogs (Nussbaum 1976; Feminella and Hawkins 1994). Our observations, however, were made in a non-fish-bearing reach of Miller Creek, 0.14 km upstream of a hanging culvert (an absolute barrier to fish), and over 5 km south and 11 km east of the local

range limit of Cope's Giant Salamander (*Dicamptodon copei*) on the eastern Olympic Peninsula; the only giant salamander species present regionally (Jones and others 2005). Oviposition habitat in our study reach, at least at the microhabitat scale, also did not appear limiting. Unimbedded boulders and cobbles, the clast sizes on which tailed frog eggs have been most often reported (Karraker and others 2006), were abundant.

The timing of oviposition in our study was similar to that reported in other studies. Rates of embryonic development reported by Brown (1975) support the conclusion that the 4 clutches we observed were laid in late July. *Ascaphus truei* oviposition has been estimated to include a range of dates extending over 2.5 mo (10 June to 29 August), with an estimated 24 July mean oviposition date (Karraker and others 2006). Based on our observations of the female that laid Clutch A, we assume that egg deposition began the day of our initial visit (29 July).

Though information on the rate of *A. truei* embryonic development is based solely on laboratory data, our data are in general agreement. We found that embryos reached the muscular response stage (stage 18) in 14 d at a mean water temperature of 12.9°C. Embryos reared in the laboratory at a constant 13.0°C required 13.2 d to reach the same stage (Brown 1975). Although Brown (1975) reported hatching at day 16 and day 13 for laboratory-reared embryos held at 13.0 and 14.5°C, respectively, we first observed hatchlings after 29 d at a mean water temperature of 13.4°C during the incubation period. This difference in timing of hatching may reflect the low temporal resolution of our observations (14–15 d intervals), fluctuations in water temperature, or both. Our hatchlings also were larger (\bar{x} = 16.9 mm) than laboratory-reared individuals measured immediately post-hatching that Wernz and Storm (1969; about 10 mm) and Noble and Putnam (1931; 13.5 mm) reported, and the 23 hatchlings measured post-preservation from a field-reared clutch in southwestern Oregon (Adams 1993; 10.5 to 12.1 mm). This difference in size, however, may simply reflect post-hatching growth of the larvae in our study because we did not know the precise date of hatching.

Few data exist on growth of *A. truei* larvae. At a constant water temperature of 11.0°C, Brown

(1975) recorded a mean growth rate (based on TL) of 0.25 mm/d for the first 4 d after hatching (or 28 to 32 d after oviposition); a maximal rate of 0.34 mm/d between 33 and 46 d after oviposition; and a decline over the next 42 d (Fig. 4). We recorded a similar decrease in growth rate following the maximal growth rate interval (Fig. 4). The significance of this pattern is unclear, but it may reflect the transition from a lipid and protein-rich yolk diet of hatchlings to the less nutritious diet of diatoms and detritus of actively feeding young larvae. Given the non-parallel intervals of growth rate data in each dataset, their similarities merit study.

Our data suggest that communal oviposition in tailed frogs and its frequency, which will depend in part on its precise definition, merits study. In headwater channels, a tradeoff exists between substrate coarsening and increased stream power as one moves downstream (Brummer and Montgomery 2003). We expect that this relationship would result in a region downstream from channel ends where reliable (perennial) and low risk (limited power) flows intersect with suitable substrates (large clast sizes) in a manner that locally favors communal oviposition. Broadening the definition of communal to beyond single rocks might have greater biological meaning, especially if the aggregation that is postulated for gravid females (Brown 1975) is not spatially highly restricted, resulting in reaches in which communal oviposition would be expected. This kind of hydrological control is not mutually exclusive to postulated predation or individual clast size controls (Karraker and others 2006) on the mode of oviposition. Additionally, our data on growth rates over the early rearing interval of *A. truei* in the wild, closely approximating growth rates from constant-temperature-reared individuals in the laboratory, provide support for the oviposition and hatching date estimation approach that Karraker and others (2006) used, at least for *A. truei*. This similarity may reflect the relatively narrow absolute temperature range of streams used for reproduction during the oviposition period; over the 71-d interval during which we made our early rearing observations, this range was 5.2°C (10.8 to 16.0°C).

Acknowledgments.—The Washington Department of Natural Resources (WDNR), through the Forest and

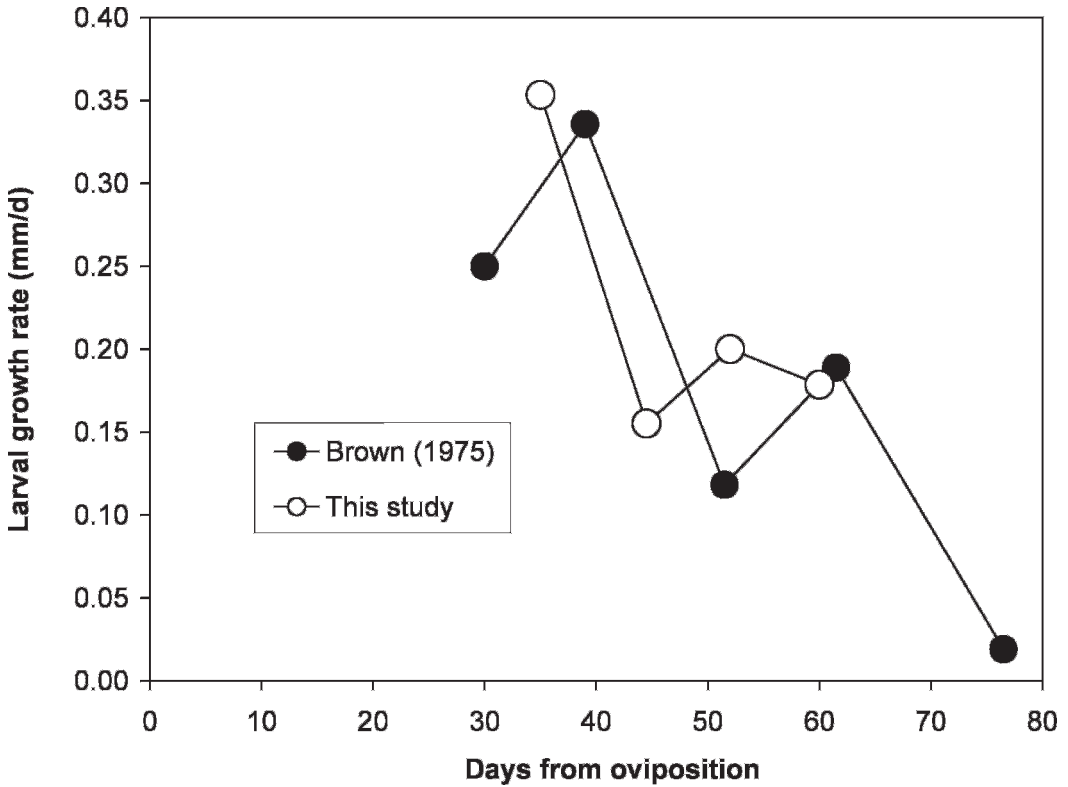


FIGURE 4. Comparison of growth rates between the constant-temperature laboratory-reared *A. truei* larvae (based on Brown 1975) and field-reared larvae. Data are plotted on the day mid-point of each growth interval for both data sets as the number of days from oviposition because the precise hatching date or date range was not known for the field-reared animals.

Fish Adaptive Management Program involving the Cooperative Monitoring Evaluation and Research Committee, the Landscape and Wildlife Advisory Group, and the Amphibian Research Consortium, funded the manipulative shade study during which these data were collected. Amphibians were handled under permits from the Washington Department of Fish and Wildlife (WDFW). The WDNR granted permission to conduct research on their lands. Lisa Hallock, Tiffany Hicks, Michael Parker, and 2 anonymous reviewers made valuable suggestions on the manuscript. This is contribution No. 25 of the WDFW Habitat Program Amphibian Research Group.

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