

Drought influences reproductive timing in two newt (*Taricha*) congeners

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Drought may have strong adverse effects on timing of pond-breeding amphibians, depending on life history traits of individual species (Matthews et al., 2013; Anderson et al., 2015). Although pond-breeding amphibians share a biphasic life history (Wilbur, 1980), selective pressures on each species may be quite different (Maiorana, 1976). The reduced hydroperiod associated with drought may affect the timing of reproduction, which in turn may have cascading trophic effects on community dynamics, such as increased interspecific larval competition, competition with other aquatic amphibians, and delayed metamorphosis (Semlitsch et al., 1988; Wilbur, 1997; Todd et al., 2010). A delay in reproduction may lead to reduced size at metamorphosis, resulting in low adult recruitment and a shift in community structure (Werner, 1986; Pechmann et al., 1989) – a condition that could, through selective pressure, lead to a shift in adult phenotypes (Wilbur and Collins, 1973; Wilbur, 1997).

The north Coast Range region of California is characterised by a Mediterranean climate: cold wet winters followed by dry, hot summers (Schoenherr, 1992). Pond and stream-breeding amphibians in this region exhibit a prolonged annual breeding season to accommodate the vagaries of annual rainfall (Storer, 1925). Two amphibians of this region characterize this flexibility in their annual breeding: the rough-skinned newt (*Taricha granulosa* Skilton, 1849), and its congener, the Coast Range newt (*T. torosa* Rathke, 1833). *Taricha granulosa* may breed anytime between

December and October (Twitty, 1966; Petranka, 1998), and *T. torosa* has been reported to breed from December to May (Stebbins, 1951). But for both species, the peak breeding season in California usually occurs in March and April (Stebbins, 1951; Riemer, 1958). *Taricha torosa* has been observed in amplexus as early as late September (Ritter, 1897), and the earliest egg deposition was recorded on 25 December in the year 1922 (Storer, 1925).

Long-term investigations of annual reproductive events for pond-breeding amphibians have revealed shifts in peak oviposition based on annual variation in atmospheric conditions (Semlitsch, 1985; Todd and Winne, 2006). Recently, shifts in peak reproductive timing have been attributed to global climate change (Blaustein et al., 2001), with amphibians in areas of warming temperatures exhibiting delayed autumnal breeding and accelerated vernal breeding (sensu Todd et al., 2010). Here we describe earlier dates of breeding and oviposition than previously reported for both of the *Taricha* species listed above.



Figure 1. *Taricha torosa* in amplexus on 15 September 2015. Note secondary sexual characters: well-developed dorsal and ventral tail fins and dark flank stripe. Photo by J.T. Wilcox.

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Figure 2. Well-developed eggs in the ovaries of *Taricha granulosa* (top) and *T. torosa* (bottom) on 20 November 2015. Photos by J.T. Wilcox.

Our observations occurred in Bonnie's Pond, a perennial stock pond on the Mitsui Ranch (38.3301°N, -122.5820°W) in Sonoma County, California, a property owned and operated by the Sonoma Mountain Ranch Preservation Foundation. Bonnie's Pond is a small (40 m diameter), deep (>3 m), spring-fed pond that exhibits extreme annual fluctuations in size but remains perennial. Bonnie's Pond is regularly surveyed: shoreline surveys are conducted, on foot, approximately once per week, and 30-minute dip net surveys are conducted at least quarterly during the year. Adults of both *Taricha* species may be found in the pond at any time of year.

On 15 September 2015, we witnessed three pairs of *T. torosa* (identified by colour pattern and relative positions of eyes to margin of head) in amplexus. All males exhibited fully developed secondary sexual characteristics, as described by Stebbins (1951) and Storer (1925), including smooth skin, swollen forearms, well-developed dorsal and ventral tail fins, and black lateral shading (Fig. 1). We returned to the pond on 20 November 2015 and observed at least four

amplexed newt pairs of both *Taricha* species, and then collected one pair of each species to assess reproductive condition. We euthanized one female of each species using buffered MS-222 (Conroy *et al.*, 2009), immersing them and allowing the agent to absorb through the skin. We then examined the internal organs to assess reproductive stage. The presence of well-developed eggs in the ovaries of both the *T. torosa* and the *T. granulosa* females confirmed that they were gravid and close to oviposition (Fig. 2).

We discovered several egg masses of *T. torosa* in late November, approximately four weeks earlier than previously recorded by Storer (1925). On 29 November 2015, the successful breeding of this species was serendipitously confirmed when a submerged fence post was removed from Bonnie's Pond and found to be clustered with *T. torosa* egg masses. We did not search the pond for the eggs of *T. granulosa* because they are deposited singly upon leaves, twigs, and other benthic substrates and are thus more difficult to detect, and searching can constitute destructive sampling. We assumed the presence of *T. granulosa* eggs because the gravid female we had examined nine days earlier had been collected in the same breeding pond, amplexed by males, and in the same state of reproductive development as the female *T. torosa*. Larvae of both species were captured in dip net surveys the following May, July, and September. At each date of capture, both species were at approximately equal stages in larval development. Our observations indicate that both *Taricha* species possess the behavioural plasticity to breed and oviposit early when conditions are optimal in an unpredictable environment (Maiorana, 1976).

Northern California recently concluded the four driest years in recorded history, from 2011 through 2014 (California Department of Water Resources, 2015). Our observations were made in the fall of 2015, just as nearly average rainfall returned to the area. Interestingly, the observation of *T. torosa* breeding in late December by Storer (1925) occurred during one of the region's most severe dry periods in more than a millennium of palaeoclimate data (California Department of Water Resources, 2015). Our observations, coupled with those of Storer (1925), demonstrate a reproductive plasticity in these newt congeners that allows them to adjust the timing of egg deposition to extreme environmental variation in rainfall. Historic droughts may have been a strong selective force in the speciation of *Taricha* over time in this region, particularly in a landscape where ponded water was an uncommon geographic feature (Schoenherr, 1992), making isolation of breeding

newts more common. Prolonged drought undoubtedly has consequences for newts in their terrestrial habitats as well, but persistence of some populations through time, in suitable habitats, indicates that their adaptation to accommodate variable rainfall amounts and patterns may prepare them well to persist in the face of global climate change.

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