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Gregory B. Pauly

Natural History Museum of Los Angeles County, gpauly@nhm.org

Katy Semple Delaney

Santa Monica Mountains National Recreation Area, katy_delaney@nps.gov

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Cover Page Footnote

We thank Lauren Scheinberg and Jens Vindum from the California Academy of Sciences for the loan of study material and Greg Schneider at the University of Michigan Museum of Vertebrates for assessing tadpole developmental stage and providing photographs from relevant specimens. Mireia Beas-Moix from the Cheadle Center for Biodiversity and Ecological Restoration at the University of California Santa Barbara and Cynthia Paszkowski of the University of Alberta Museum of Zoology kindly provided museum specimen information. We also thank Steve Goldberg for providing an early draft of his manuscript and for helpful conversations about anuran breeding activity.

Late-season Reproduction in Western Toads (*Bufo boreas*)

Gregory B. Pauly^{1*} and Katy Semple Delaney²

¹*Urban Nature Research Center and Section of Herpetology, Natural History Museum of Los Angeles County, Los Angeles, CA 90007*

²*Santa Monica Mountains National Recreation Area, 401 W. Hillcrest Drive, Thousand Oaks, CA 91360*

Western toads (*Bufo boreas*, or *Anaxyrus boreas* of some authors) typically breed from late January to July depending on elevation, latitude, and local conditions (Sornborger 1979; Stebbins 2003; Thompson 2004; Muths and Nanjappa 2005). Generally, breeding takes place early in the active season and is explosive with the breeding season lasting only a few weeks with most of the breeding activity occurring in a few nights (Sornborger 1979; Olson et al. 1986; Muths and Nanjappa 2005; Pauly pers. obs.). At low elevation sites in Southern California, for example, breeding may begin as early as late January assuming rainfall has been adequate to fill breeding sites and stimulate activity. At higher elevation sites, breeding activity is triggered by warming conditions and snowmelt with toads breeding shortly after emerging from hibernation sites (Sornborger 1979; Olson et al. 1986; Fetkavich and Livo 1998; Hammerson 1999; Thompson 2004; Muths and Nanjappa 2005).

Here we report unusually late breeding activity in western toads. On 9 November 2015, one of us (KSD) observed late stage tadpoles (up to Gosner Stage 43) at a seasonal pond in the Los Robles Open Space, Santa Monica Mountains, Ventura County, California (34.163226, -118.881964, elevation 370 m; Figs. 1, 2). The pond is oval with maximum size of 7 m by 5 m. No metamorphs were observed in the surrounding terrestrial habitat, but the presence of many tadpoles undergoing metamorphosis suggests that this late breeding event would result in metamorphs leaving the pond within a few days. Photographs of these tadpoles were submitted to the Reptiles and Amphibians of Southern California (RASCals) Citizen Science Project (iNaturalist 2365499) with additional photographs deposited in the Natural History Museum of Los Angeles County Photographic Collection (LACM PC 1998–2005).

Breeding was likely triggered by an unusually large rain event on the morning of 15 September 2015 that filled this previously dry, temporary pond. This rain event resulted in part from low-level moisture from the former Eastern Pacific Hurricane Linda. Weather data from Los Angeles indicate the storm produced the second wettest September day on record (6.07 cm). Data from the nearest weather station in the Santa Monica Mountains, which is at Deals Flat, ca. 11.5 km southwest of the breeding site, are available via climateanalyzer.org. At Deals Flat, 3.3 cm of rain fell in this unusual storm event, which is more rain than fell in the previous February (2.18 cm) or March (1.78 cm) when *B. boreas* typically breeds in this area. The rain event also took place in the fourth year of a severe drought in Southern California, during which time *B. boreas* breeding activity was greatly reduced.

To the best of our knowledge, the occurrence of tadpoles in November and an inferred breeding date in mid-September are the latest observations of breeding activity reported for *B. boreas*. Lemm (2006) noted that western toads breed from January to September, a slightly longer period than the January to July period suggested by Stebbins (2003), but no dates or locations of

* Corresponding author: gpauly@nhm.org



Fig. 1. Western toad (*Bufo boreas*) breeding pond observed 9 November 2015 in the Los Robles Open Space, Santa Monica Mountains, Ventura County, California. Note the ring of toad tadpoles lining the pond's edge (LACM-PC 2001).

September breeding activity were provided. Lemm (pers. comm.) could not reference specific observations of September breeding activity although he was certain he observed amplexant *B. boreas* in Southern California in September, with these individuals likely observed in the deserts. The latest specific observations of breeding activity are from August. Fetkavich and Livo (1998) reported late-season breeding in the southern Rocky Mountains with a clutch likely laid the first week of August 1997, though no tadpoles were suspected of surviving the winter. Sornborger (1979) also reported late-season breeding in *B. boreas*, this time at a high elevation site in the San Jacinto Mountains of Southern California. Here the primary breeding activity was in late April 1977, with subsequent breeding activity after a major storm event 15–17 August 1977 (19.3 cm of rain). Survivorship of these late-season tadpoles was not fully tracked, but mortality was suspected to be high due to the onset of cold weather.

A review of museum specimens also failed to find evidence of breeding as late as observed at the Ventura County pond. A search of the VertNet database for all *B. boreas* tadpoles returned 471 records (search conducted by requesting all *Bufo boreas* and *Anaxyrus boreas* records with the terms “tadpole OR tadpoles OR larva OR lot” and then eliminating any records that could not be confidently assigned as tadpoles). The latest collection month reported was September, for which there were seven lots (1.5% of total records): CAS 206431 and 206432 from 1 September 1998; CAS 209911 from 8 September 1999; UMMZ 151566 from 10 September 1962; CAS 180323 from 13 September 1991; UMMZ 151568 from 13 September 1967; and CAS 242852 from 16 September 2002. Photographs or specimens of these seven lots were examined to assess developmental stage following Limbaugh and Volpe (1957) and Gosner (1960). Based on developmental stage and collection date, the two latest season records are stage 24–25 tadpoles collected 13 September 1991 (CAS 180323) and stage 27–34 tadpoles collected 16 September



Fig. 2. Late-season western toad (*Bufo boreas*) tadpoles and early-stage metamorphs (up to Gosner Stage 43) observed 9 November 2015 in Ventura County, California (LACM-PC 2004 and iNaturalist 2365499).

2002 (CAS 242852). Both of these lots were collected in Southern California from relatively low elevation sites (1060 m and 775 m, respectively).

The Ventura County tadpoles were observed 9 November 2015, nearly two months later than available late-season tadpole records. Although this observation is much later in the season, it is possible that the Ventura County tadpoles and the two latest specimen records (CAS 180323 and CAS 242852) all result from breeding activity in September. Breeding dates for these records cannot be accurately estimated from developmental stage because development is strongly correlated with temperature and therefore will vary based on local conditions such as air temperature, percent shade, and pond vegetation and substrate. However, by generalizing based on developmental rates estimated by Limbaugh and Volpe (1957), it is possible that both CAS 180323 and 242852 resulted from early September breeding events. Breeding activity at the Ventura County pond was still later than that for these museum records because it likely occurred 15–17 September 2015, immediately after the large rain event.

Goldberg (2016) examined gonads of museum specimens collected between February and August from multiple localities in Riverside County, California, all more than 145 km east of the Ventura County pond and in much drier habitat with more variable summer rainfall. All adult males and females had mature gametes and could be reproductively active during this 7-month period. Although samples from September were not available, Goldberg suggested that the long activity period was consistent with a continuous pattern of reproduction in which individuals have prolonged periods of breeding readiness allowing them to take advantage of favorable

conditions if they arise. This suggestion is consistent with our review of tadpole specimens as all seven lots collected in September likely resulted from late-season breeding activity, in which individuals bred long after the primary breeding period for that region.

This new record, in combination with our review of museum specimens and published reports (Sornborger 1979; Fetkavich and Livo, 1998; Lemm 2006; Goldberg, 2016), documents that *B. boreas* has a prolonged period of breeding readiness that can extend at least into mid-September. Thus, although most breeding activity occurs early in the active season, western toads are capable of breeding later in the year. At higher elevations, late-season breeding is unlikely to allow tadpoles adequate time to reach metamorphosis (e.g., Sornborger 1979; Fetkavich and Livo 1998), but at lower elevations in the southern portion of the range, late season breeding has a higher chance of tadpoles successfully completing metamorphosis, as likely occurred for the Ventura County tadpoles. The western spadefoot (*Spea hammondi*), which shares a similar distribution as *B. boreas* in Southern California, also has been found to have a more continuous reproductive mode allowing it to take advantage of rainfall events outside of the primary breeding period (Ervin et al. 2005; Ervin and Cass 2007).

In typical years in coastal Southern California, western toads breed during the late winter and spring rains. In spring 2015, however, rains were abnormally low due to drought conditions, and there was very little breeding activity in the region (based on long-term monitoring of sites in and around the Santa Monica Mountains National Recreation Area and by the low number of tadpole and metamorph observations submitted to the RASCals project). As a result, some adult toads likely had mature gametes and were capable of breeding following the atypical late-season rain event. Another possibility is that western toad females are capable of producing multiple clutches in a single breeding season, with breeding activity during the primary breeding season and a second clutch months later following storm events. We don't think this occurred here given the relatively dry spring and the low levels of breeding activity observed across Southern California. Among Nearctic *Bufo*, multiple clutches have only been documented in *Bufo cognatus* (Krupa, 1986). Nevertheless, future studies should investigate this possibility, particularly in areas with mild winters where late-season breeding is more likely to yield tadpoles that successfully reach metamorphosis.

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We thank Lauren Scheinberg and Jens Vindum from the California Academy of Sciences for the loan of study material and Greg Schneider at the University of Michigan Museum of Vertebrates for assessing tadpole developmental stage and providing photographs from relevant specimens. Mireia Beas-Moix from the Cheadle Center for Biodiversity and Ecological Restoration at the University of California Santa Barbara, Brad Hollingsworth at the San Diego Natural History Museum, and Cynthia Paszkowski of the University of Alberta Museum of Zoology kindly provided museum specimen information. We also thank Steve Goldberg for helpful conversations about anuran breeding activity.

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