

Atypical Anuran Amplexus between Western Spadefoot and Pacific Chorus Frog During an Explosive Breeding Event, in Fresno County, CA

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Amplexus between different species of anurans, anurans and non-amphibians, anurans and inanimate objects, and live anurans and dead conspecifics has been reported worldwide, and reviewed (Pearl et al. 2005, Serrano et al. 2022a, 2022b, Alvarez, in review). These interactions have been variously reported with characterizations that include several dozen different words used to describe the behavior, including but not restricted to interspecific amplexus, heterospecific amplexus, hybridization, reproductive interference, Davian behavior, reproductive behavior, misdirected amplexus, and many other terms. Alvarez et al. (in review) summarized nearly 300 accounts of atypical amplexus and suggested nomenclature that would best describe all forms of atypical amplexus into three groups: interspecific amplexus, misdirected amplexus, and Davian behavior. Here we report on atypical amplexus that is interspecific and misdirected between a declining amphibian, the Western Spadefoot (*Spea hammondii*), and a commonly syntopic amphibian, the Pacific Chorus Frog (*Pseudacris regilla*).

During rain events that occurred on February 2 and 3, 2024, we conducted surveys of several vernal pools in Fresno County where we had previously observed

Western Spadefoot breeding, or suspected their presence. We approached pools during evening surveys with hand-held flashlights. These pools had choruses of Western Spadefoot that attracted our attention and which we investigated closely with the goal of detecting the presence and recording breeding activity of the species as part of a broader investigation into the species by the senior author.

We observed Western Spadefoot adults calling from the pool and several individuals appeared to be in amplexus. A closer investigation resulted in observations of several interspecific amplexal events made up of single Western Spadefoot adult and an amplexing male Pacific Chorus Frog. On two occasions, the Western Spadefoots were later identified as female as they were laying eggs while in amplexus with a chorus frog. The interspecific pairs moved around in 0-15 cm deep pools during the 1 hr observation time. Observations ended shortly after egg laying appeared to be complete.

We noted that at least two interspecific amplexing pairs, one on each night of observation, was in inguinal position (see Duellman and Trueb 1994; Fig. 1), where the chorus frog was grasping the waist of the Western

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Fig. 1. An adult male Pacific Chorus Frog (*Pseudacris regilla*) in inguinal amplexus with an adult female Western Spadefoot (*Spea hammondii*), in Fresno County, CA. Photo by D. Hardeman Jr.

Spadefoot—considered misdirected amplexus by Alvarez et al. (in review). In two additional amplexing pairs of spadefoot and chorus frogs, we noted they were in axillary amplexus (see Duellman and Trueb 1994; Fig. 2), which is considered typical for members of the family Hylidae (Halliday and Alder 2002, Wells and Schwartz 2007, Ethier et al. 2021).

Amplexus is a component in most anuran species and consists of a male grasping a female from behind with his forelimbs. Thus, not surprisingly, it has been interpreted as a behavior by which a male ensures the fidelity of its female partner during reproductive activity, increasing the chance of egg fertilization only by the amplexing male (Duellman and Trueb 1994, Wells and Swartz 2007, Carvajal-Castro et al. 2020). Sexual dimorphism can impose physical restrictions in some species, dictating the method by which males amplex (i.e., axillary, inguinal, cephalic, etc.; Duellman and Trueb 1994) whereby both individuals must appropriately align their respective cloacas so that egg fertilization is optimized (Davis and Halliday 1977, Robertson 1990, Carvajal-Castro 2020). Consistent with other genera in the Hylidae family, *Pseudacris* species typically perform axillary amplexus. The male mounts the female, grasps her directly behind the forelimbs, with the male cloaca positioned above the female cloaca (Wells and Schwartz 2007, Halliday and Adler 2022). Our observations suggest that the morphometric differences in Western Spadefoot and Pacific Chorus Frogs necessitated inguinal amplexus in at least two instances.

Different selective pressures are known to shape the behavioral, physiological, and morphological traits that characterize the diverse reproductive modes and behaviors in anurans in comparison to other vertebrates (Carvajal-Castro et al. 2020). This becomes particularly true when two species, closely related or not, are explosive breeders, and are syntopic at the time of breeding. Males of explosive breeding species that gather in dense aggregations may engage in “scramble competition,” which results in attempting amplexus with any individual, and struggling among themselves for possession of females (Wells 1977).

In the case we report here, both chorus frogs and spadefoots are explosive breeders, taking advantage of rain events and breeding in small, temporary pools (Stebbins 1954). Their behavioral ecology supports a need to amplex a potential mate prior to a competitor, potentially resulting in misdirected or interspecific amplexus. D’Amore et al. (2009) suggested that this type of atypical amplexus may be an evolutionary trap in that a declining species has a decreased chance of successful reproduction when interference occurs during the breeding event. Magnhagen (2003) and Alvarez (2011) added that amplexing pairs, particularly atypical amplexing individuals, may also increase predation potential by slowing the moment or escape ability of one of both animals. Further,

close interaction between interspecific pairings may also increase a risk of exposure and transmission of chytridiomycosis to one or both individuals. This should be considered when research is conducted on populations of anurans that are known to be infected by chytridiomycosis, ranavirus, or other pathogens (Rowley and Alford 2007, González-Mollinedo and Mármol-Katrán 2019).

We suspect that the female Western Spadefoot that we observed expelling eggs while amplexed by an interspecific male fell into an ecological trap in that her eggs were not likely fertilized, decreasing or eliminating any chance to reproduce in 2024. It isn’t clear how these two species reduce or avoid scramble competition when breeding at the same site during the same periods of time. We speculate that this type of syntopic occurrence is uncommon, with Pacific Chorus Frogs breeding over a longer period with fewer events that result in high intensity competition, while the spadefoot adults will typically breed during a shorter period and perhaps avoid or decrease interspecific amplexus by breeding slightly later in the season. We note, however, that in small isolated vernal pools, that may fill during a specific rain event, this behavior may occur with some level of frequency that may decrease reproductive output of Western Spadefoot, which is in decline throughout its range (Tompson et al. 2015).

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Fig. 2. An adult male Pacific Chorus Frog in axillary amplexus with an adult female Western Spadefoot, in Fresno, County, CA. Photo by H. Isner.