Davian behaviour in the threatened California red-legged frog *Rana draytonii*: more than just a waste of time

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Davian behaviour, also variously referred to as necrogamy (Bettaso et al., 2008), necrophilia (Cortés Bedoy et al., 2014), and misdirected copulation (Ayres, 2010), is an event during which a live individual attempts to mate with a dead individual for reproductive gain (Ayres, 2010). This behaviour has been observed in amphibians (Bettaso et al., 2008), reptiles (Costa et al., 2010), birds (Lehner, 1988), and mammals (Dickerman, 1960), but appears to be most common among anurans (Pearl et al., 2005). Alvarez (2011) reported Davian behaviour between a western toad (*Bufo boreas*) and California red-legged frog (*Rana draytonii*); that observation, however, would have been more appropriately referred to as interspecific amplexus because neither individual was dead. Herein we report two observations of Davian behaviour in the threatened California red-legged frog.

In 2001, while conducting daytime monitoring surveys to assess reproduction in California red-legged frogs within mitigation wetlands in Contra Costa County, California, USA, the senior author encountered a live adult male California red-legged frog in pectoral amplexus with a dead adult female conspecific (Fig. 1). The pair was photographed but not handled. Amplexus occurred along the water’s edge (approximately 5 cm from the pool edge and in water 2 cm deep), and adjacent to a patch of cattail (*Typha* sp.). When encountered, the male was clasped tightly to the female’s thoracic region. The female was in a very early state of decomposition, and showed evidence of having been ovipositing at death, or that eggs had been forced outward by the compressive force of the male.

In 2016, we were again conducting daytime monitoring surveys in a drain adjacent to the first observation when we similarly encountered a live adult male California red-legged frog in pectoral amplexus with a dead adult female conspecific. Amplexus was observed along the water’s edge (approximately 30 cm from the pool edge and in water 20 cm deep), amidst a patch of dead cattail (*Typha* sp.). The small adult male was clasped very tightly to the female’s thoracic region. The female was partially decomposed, with a thin film of fungal hyphae covering the majority of her body (Fig. 2). Despite handling and photography, the male did not disengage from the female.

Davian behaviour has been considered a possible ecological trap because persistent necrophilic males may lose or experience diminished opportunities to successfully reproduce during the (often brief) breeding season (Ayres, 2010). Magnhagen (2003) suggested that the risk of predation may also increase during Davian behaviour due to the lengthy hyperfocus of the male. This contention is supported by our observation, in that neither the proximity of the four observers (in the 2016 event) nor a brief period of photography (2001) disturbed the respective males. Risk of predation rises even more if, as in these examples, the behaviour occurs during daylight and in shallow water.
Under some circumstances there might be potential gains from Davian behaviour as at least in the beaked toad (*Rhinella proboscidea*) necrophilic males may be able to squeeze eggs from dead females and fertilise them (Izzo et al., 2012). This occurrence may be rare as it has not been reported for other species. Our 2001 observation did include a small (20-25) number of ejected eggs at the cloaca of the female California red-legged frog. We made no attempt to determine if these eggs were fertilised. In the case of California red-legged frogs, however, females typically attach the egg mass to vegetation at or near the surface (Storer, 1925; Alvarez et al., 2013) in water that is, on average, 38 cm deep (Alvarez et al., 2013). In this case, the ejected eggs, which would typically number 2,000 to 6,000, were resting on the hind legs of the dead female in water approximately 2 cm deep. If this small number of eggs were fertilised, we contend that the conditions were not appropriate for their development, resulting in no fitness gains for the male or female.

Alvarez (2011) reported male western toads, a sympatric species with California red-legged frog in amplexus with a variety of objects, including a root ball, cattle dung, a dead conspecific, and a live female *R. draytonii*. Bateson (1983) suggested that an explosive breeding reproductive strategy, as in the western toad, may contribute to misdirected amplexus, including necrogamy (i.e., Davian behaviour). As the California red-legged frog is not considered an explosive breeder, it follows (sensu Bateson, 1983) that Davian behaviour would be expected to be less common in this species. Our temporally-spaced observations of Davian behaviour in 2001 and 2016, on a site where breeding-season California red-legged frog surveys are conducted annually, suggests that it is not common; we calculated a rate of observation at less than 0.0003 %. Alvarez (2011) suggested that temporally compressed breeding events, which periodically occur at this site due to prolonged drought, may result in increased breeding pressure from conspecifics and sympatric anurans, thereby contributing to misdirected amplexus behaviour (i.e., non-conspecifics) by males. Inasmuch as Davian behaviour may represent an ecological trap for some individuals, it also represents a confounding stressor on a threatened species.

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