



Developmental onset of escape-hatching responses in red-eyed treefrogs depends on cue type



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Hatching is an essential and often behaviourally mediated process. Many animals can hatch at different developmental stages, and embryos time hatching based on cues indicating threats to eggs or opportunities outside them. However, specific mechanisms enabling such responses, and how their ontogenies combine to determine when environmentally cued hatching is possible, are largely unknown. Many embryos use hatching cues in multiple sensory modalities. Thus, comparing response onset across cue types can distinguish shared ontogenetic constraints, such as hatching ability, from modality-specific constraints, such as sensor development. The arboreal embryos of red-eyed treefrogs, *Agalychnis callidryas*, hatch rapidly in response to physical disturbance in predator attacks and hypoxia if flooded. Prior research documented both responses beginning at age 4 days. Because embryos orient in oxygen gradients long before this, we hypothesized the onset of hypoxia-cued hatching is limited by development of hatching ability. The onset of mechanosensory-cued hatching might share this constraint or be limited by a later-developing sensory mechanism. We tested developmental series for hypoxia-cued hatching, by submerging eggs in degassed water to impose strong hypoxia, and for mechanosensory-cued hatching, by manually jiggling eggs as a simulated attack. We identified morphological markers to distinguish developmental stages across the onset of hatching. Hatching competence begins substantially earlier than previously reported. Across sibships, hypoxia-cued hatching began at a smaller size and less developed stage, and on average 8 h earlier than mechanosensory-cued hatching. Both responses increased from 0% to 100% over just a few hours. Latency to hatch after stimulation was longer in hypoxia-cued hatching and uncorrelated with stage, whereas latency in mechanosensory-cued hatching decreased with development. Hypoxia-cued hatching appears constrained by the development of hatching ability, while mechanosensory-cued hatching appears constrained by mechanosensor development. Hatching ability is not the sole constraint on the onset of escape-hatching responses to attacks. © 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Developmental changes in behaviour reflect a combination of maturational processes and ontogenetic adaptations (Wiedenmayer, 2009). For instance, the sequential development of different sensory systems increases the range of stimuli to which animals can respond (Romagny, Darmaillacq, Guibe, Bellanger, & Dickel, 2012), and the appropriate response to a potential threat changes with ontogenetic changes in vulnerability (Wiedenmayer, 2009). Most research on the development of behaviour in embryos

focuses on behaviours that will function later in life, including motor skills (Bate, 1999; Grillner, 2000), communication (Colombelli-Negrel et al., 2012; Lickliter, 2005), antipredator defence (Ferrari & Chivers, 2009; Mathis, Ferrari, Windel, Messier, & Chivers, 2008) and foraging (Darmaillacq, Lesimple, & Dickel, 2008; Guibe, Poirel, Houde, & Dickel, 2012). Nevertheless, embryo behaviour is of widespread and immediate functional consequence in one context: hatching. Both embryos and hatchlings often suffer high mortality, but causes of death (e.g. predators, pathogens, harsh abiotic conditions, starvation) are frequently stage specific (Warkentin, 2011a, 2011b). Thus embryos can avoid or escape from threats, and exploit opportunities, by timing their hatching

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appropriately. Environmentally cued hatching (ECH) is widespread among animals (Warkentin, 2011a); embryos respond to diverse biotic and abiotic factors — including predators, pathogens, conspecifics, hosts, food resources, dehydration and flooding — using cues in multiple sensory modalities (Warkentin, 2011a, 2011b). Responses range from substantially premature hatching, to escape threats to eggs, to long delays in hatching under conditions unfavourable to hatched young. Nevertheless, there must be constraints on the developmental period when hatching is sensitive to environmental cues.

The factors that limit the period of cued, plastic hatching depend on the type of ECH. For instance, for embryos that delay hatching until conditions are favourable, energy reserves can limit the maximum delay (Bradford & Seymour, 1985; Darken, Martin, & Fisher, 1998). For embryos that hatch early in response to cues, two factors may constrain the onset of hatching responses. First, embryos must have reached hatching competence in order to show a hatching response to any cue. The development of any component of the hatching mechanism could, therefore, limit the onset of cued hatching, and this constraint would apply equally across all cue types. Second, embryos must detect an environmental cue in order to respond to it. Cue detection depends on the development of the relevant sensory system, and cue assessment may also require further neural processing (Romagny et al., 2012; Wiedenmayer, 2009). Thus, the developmental stage when embryos begin responding to threats may differ for cues in different sensory modalities. We studied the ontogenetic onset of an early 'escape-hatching' response to two different threats, cued by two sensory modalities, to test whether they shared or differed in their period of sensitivity, and thus were limited by development of the same or different aspects of the underlying mechanisms.

We worked with red-eyed treefrogs, *Agalychnis callidryas*, one of the best-studied examples of environmentally cued hatching. This species lays eggs on vegetation over ponds, where undisturbed embryos develop for 6–7 days before they hatch and drop into the water below. Hatching is a rapid switch between two environments, allowing embryos to escape egg-stage threats by hatching early. Egg predation is the most common threat; snakes have attacked from 24% to over 60% of monitored clutches, across years and ponds, while wasps attacked up to 50% of clutches (Gomez-Mestre & Warkentin, 2007; Warkentin, 1995, 2000b). Embryos can hatch in seconds up to 30% prematurely to escape from attacking snakes and wasps (Warkentin, 1995, 2000b). They also hatch early, but less synchronously, in response to the slower-acting threats of pathogenic fungus and dehydration (Salica, Vonesh, & Warkentin, 2012; Warkentin, Currie, & Rehner, 2001). Furthermore, submergence underwater can be deadly for eggs not yet capable of hatching (Pyburn, 1970) and elicits hatching within tens of minutes (Warkentin, 2002). Hatching responses to these different threats are mediated by different cue types, in different sensory modalities. Predator-induced hatching depends on mechanosensory cues, including vibrations, during the physical disturbance of clutches, and embryos can distinguish snake vibrations from those caused by benign sources (Warkentin & Caldwell, 2009; Warkentin, 2005). In contrast, flooding-induced hatching is cued by hypoxia (Warkentin, 2002, 2007). As early as the neural tube stage, long before hatching has been observed, embryos sense and orient in oxygen gradients within the egg (Rogge & Warkentin, 2008). Thus we hypothesize that the onset of flooding-induced hatching is limited by the development of hatching ability rather than oxygen-sensing ability. The sensory system mediating predator-induced hatching is unknown; however, mechanosensory structures in anurans include the inner ear and lateral line (Hill, 2008), both of which develop later (Bever, Jean, & Fekete, 2003; Nieuwkoop & Faber, 1956). Thus the onset of predator-induced

hatching might be limited by the development of either hatching ability or mechanosensory ability.

Agalychnis callidryas shows very little additive genetic variance for the onset of hatching in response to physical disturbance; this suggests a developmental constraint, hypothesized to be the maturation of the hatching mechanism (Gomez-Mestre & Warkentin, 2013). A comparative study of the onset of hatching competence across *Agalychnis* species and other phyllomedusid treefrogs used both flooding and mechanosensory cues concurrently, without testing for a possible difference in the response to them (Gomez-Mestre, Wiens, & Warkentin, 2008). In Gamboa, Panama, escape-hatching begins on the morning embryos are 4 days old, both in field observations of predation and flooding and in predation and pathogen experiments (Gomez-Mestre & Warkentin, 2013; Gomez-Mestre et al., 2008; Warkentin, 1995, 2000b; Warkentin, Buckley, & Metcalf, 2006; Warkentin et al., 2001). Work at other sites shows some geographical, possibly thermal, variation in the onset of hatching but has been, nevertheless, consistent with the hypothesis that hatching onset is limited by development of the hatching mechanism (Gomez-Mestre & Warkentin, 2013; Gomez-Mestre et al., 2008; Warkentin, 1995).

However, an embryo's experience of hypoxia and risk of mortality in flooding must depend substantially on both the aquatic oxygen level and the exposed surface area of the egg. Thus, to test for congruence or divergence in the onset of hatching across cue types, and the possibility that different traits limit the onset of responses to different cues, we developed a stronger, more consistent assay for hypoxia-cued hatching. First, we exposed a developmental series of embryos to this strong hypoxia cue and found the escape-hatching response begins substantially earlier than revealed in any prior research. Then, with a second developmental series, we assessed the ontogenetic onset of both hypoxia-cued hatching and mechanosensory-cued hatching in the same sibships. We also tested for developmental changes in latency to hatch in response to both cues. Finally, because El Niño weather during the second series may have altered the timing of development and hatching, we tested a third developmental series with mechanosensory cues the following year to assess the developmental consistency of response onset.

Standard staging tables (Gosner, 1960; Pyburn, 1963) offer no resolution of developmental variation across the hatching period in *A. callidryas* (Warkentin, 2000a, 2002). Embryos pass through 22 stages in 4 days; then, over the next 3–4 days, from the earliest predator-induced hatching to the latest spontaneous hatching, they remain in stage 23 (Gosner, 1960; Warkentin, 2002). Stage 23 ends when external gills regress, which depends on hatching timing (Warkentin, 2000a, 2002, 2007). During the plastic hatching period there is, however, substantial growth and development of mouthparts, digestive system, lungs and other structures (Warkentin, 1999b). Our prior time-based methods for characterizing development have revealed ecologically important changes across the plastic hatching period, affecting viability, survival with aquatic predators and onset of feeding (Touchon, McCoy, Vonesh, & Warkentin, 2013; Warkentin, 1995, 1999a, 1999b; Warkentin, Buckley, et al., 2006; Willink, Palmer, Landberg, Vonesh, & Warkentin, 2014). Nevertheless, they offer insufficiently detailed developmental resolution for the study of mechanisms underlying changes in embryo behaviour. Therefore, in the second developmental series, we photographed test animals to identify characters that could be used as markers of development across the onset of cued hatching responses. This is a step towards a detailed staging table across the entire period of hatching competence and, together with our cued hatching tests, should make the onset of cued hatching abilities morphologically identifiable.

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