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SYMPOSIUM

Plasticity of Hatching in Amphibians: Evolution, Trade-Offs, Cues and Mechanisms

Karen M. Warkentin1,*,†

*Department of Biology, Boston University, 5 Cummington Street, Boston, MA, 02215, USA; †Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Panamá, República de Panamá

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1E-mail: kwarken@bu.edu

Synopsis
Many species of frogs and salamanders, in at least 12 families, alter their timing of hatching in response to conditions affecting mortality of eggs or larvae. Some terrestrially laid or stranded embryos wait to hatch until they are submerged in water. Some embryos laid above water accelerate hatching if the eggs are dehydrating; others hatch early if flooded. Embryos can hatch early in response to predators and pathogens of eggs or delay hatching in response to predators of larvae; some species do both. The phylogenetic pattern of environmentally cued hatching suggests that similar responses have evolved convergently in multiple amphibian lineages. The use of similar cues, including hypoxia and physical disturbance, in multiple contexts suggests potential shared mechanisms underlying the capacity of embryos to respond to environmental conditions. Shifts in the timing of hatching often have clear benefits, but we know less about the trade-offs that favor plasticity, the mechanisms that enable it, and its evolutionary history. Some potentially important types of cued hatching, such as those involving embryo–parent interactions, are relatively unexplored. I discuss promising directions for research and the opportunities that the hatching of amphibians offers for integrative studies of the mechanisms, ecology and evolution of a critical transition between life-history stages.

Introduction
Amphibians have evolved great reproductive diversity, varying in the size and structure of their eggs and egg masses, the sites at which they deposit their eggs, the level of parental care they provide, and the amount of development that happens before hatching (Salthe 1963; Altig and McDiarmid 2007; Wells 2007). Across this diversity, embryos all begin life surrounded by a vitelline membrane and a gelatinous egg capsule. Egg capsules and egg masses mediate embryos’ interactions with the outside world, offering protection and imposing constraints (Seymour and Bradford 1995; Warkentin, this volume). Hatching, when embryos exit from their egg capsules, changes both the physical environment of developing amphibians and their biotic interactions. It is a major transition between life stages, comparable to metamorphosis. A rich body of research on complex life cycles has focused on metamorphosis; however, the general theory developed to understand transitions between life stages should also apply to hatching. This theory focuses on trade-offs between costs and benefits, or risks and opportunities, across life-stages, often measuring these in terms of size-specific rates of mortality and growth at each stage (Werner 1986; Benard 2004).

Our current understanding of metamorphosis is that it is fundamentally plastic (Benard 2004; Pechenik 2006). The timing of metamorphosis and the body size at which it occurs vary with multiple environmental factors. The magnitude of these effects vary substantially and some effects are adaptive while others are not. However, invariant size at or timing of metamorphosis seems more likely to be a result of canalization in particular cases than to be the general condition or ancestral state. Hatching may also be inherently plastic. However, it differs from
metamorphosis in some ways that are relevant if we wish to apply to hatching the theory developed for metamorphosis.

The most important difference has to do with how we assess costs and benefits. Amphibian embryos and many newly hatched larvae do not eat. Developing embryos basically absorb water and re-organize the resources provided by the egg. Moreover, they do not lose access to those resources at hatching; they carry their remaining yolk reserves into posthatching life. This is fundamentally different from metamorphosis to effect changes in environmental conditions modify the fundamental details of development. Studies of hatching, therefore, need to attend to the conditions (Warkentin, this volume). Ecological constraints both the period when hatching begins after hatching, costs and benefits both might be more appropriately measured as functions of development, rather than as functions of size per se. Variation in hatching size is limited by egg size, whereas size at metamorphosis can vary dramatically. Metamorphosis is itself a change in form; postmetamorphic animals are, by definition, at the same developmental stage and vary less in shape than they do in size. Hatching is not a change in form; however, it often occurs while form, needs, and abilities are developing rapidly. Because of this, development can strongly affect levels of risk and opportunities in the egg and in posthatching environment (e.g., Warkentin 1999; Rogge and Warkentin 2008). In addition, development mechanistically constrains both the period when hatching can occur and what embryos are capable of perceiving, thus limiting potential responses to environmental conditions (Warkentin, this volume). Ecological studies of hatching, therefore, need to attend to the details of development.

We have a much better understanding of how environmental conditions modify the fundamental mechanisms of metamorphosis to effect changes in its timing (e.g., Denver 1997, 2009) than we do of the mechanisms that effect changes in the timing of hatching. Two types of mechanisms of hatching are known in amphibians (reviewed by Duellman and Trueb 1986). The most common is chemical; many species that hatch as larvae have glands on the head (hatching or frontal glands) that release proteolytic enzymes that digest components of the egg membrane, weakening it (e.g., Yamasaki et al. 1990; Nokhbatatofoghahai and Downie 2007). Muscular activity may rupture the weakened membrane, but hatching can occur without it (Carroll and Hedrick 1974; Touchon et al. 2006). Hatching may also be mechanical; some direct-developing frogs use an egg tooth to physically rupture their capsules. In many salamanders, early embryos hatch from the vitelline membrane into a capsular chamber, from which a second stage of hatching occurs much later in development (Salthe 1963). In some anurans, outer capsular layers split and inner capsules emerge from them, probably due to differential swelling, well before embryos hatch (Duellman and Trueb 1986). How amphibians alter their mechanisms of hatching in response to environmental cues to effect changes in the timing hatching is still largely unknown.

Information on environmentally cued hatching (ECH) across amphibian species varies from richly documented cases in which we understand many aspects of the mechanisms, function, and evolutionary history of cued hatching, to individual experimental studies demonstrating variation in hatching in response to a particular environmental variable, to anecdotal field-observations indicating hatching patterns worthy of further study. Nonetheless, it is clear that ECH occurs in many, diverse amphibians, in multiple environmental contexts, and that embryos show a variety of types of response involving different cues and mechanisms. I first review the phylogenetic distribution and environmental contexts of cued hatching across amphibians, then consider the evolution of hatching plasticity, the selective trade-offs that favor it, the types and specificity of cues that mediate responses to environmental factors, and future directions for research.

**Responses to abiotic factors affecting survival of embryos or hatchlings**

Oxygen and water are both vital for development and their supply is strongly affected by conditions outside the egg. Either dehydration or hypoxia can kill early life-stages but the risks vary across hatching and there are often trade-offs. The evolution of terrestrial eggs frees embryos from boundary layers of still water that impede gas exchange, but allows
evaporative water loss. Traits that reduce water loss, such as close packing of eggs in terrestrial masses, also limit oxygen supply (Seymour 1999). Thus, egg capsules both protect embryos from desiccation and limit their oxygen supply; hatching frees larvae from the diffusion barrier of the capsule but increases their vulnerability to dehydration and their dependence on external water supplies. Amphibian embryos time hatching in relation to levels of oxygen and water in several contexts.

There are multiple origins of terrestrial eggs that wait for flooding to hatch (Fig. 1). Most mole salamanders, Ambystomatidae, have aquatic eggs but *Ambystoma opacum* and *A. cingulatum* independently evolved terrestrial eggs that hatch when flooded (Anderson and Williamson 1976; Petranka 1998). Depending on the timing of flooding, embryonic periods can vary from 2 weeks to over 100 days (Jackson et al. 1989) (Fig. 2 and Supplementary Table S1). Hypoxia, rather than submergence per se, is the cue that stimulates hatching (Petranka et al. 1982). Another mole salamander, *A. gracile*, lays eggs that can be exposed to air when water levels in ponds drop. Emergent eggs survive well and eventually hatch but exposure to air appears to delay hatching; most eggs in clutches that were experimentally re-flooded after either 20 or 31 days in air hatched within a day of submergence (Marco and Blaustein 1998). All hatchlings were similar in size and developmental stage, regardless of the duration of their exposure to air, suggesting slowed development during this period. Terrestrially incubated eggs that wait for flooding to hatch also occur in *Amphiuma means* (Gunzburger 2003) and, apparently, in populations of the plethodontid *Eurycea quadridigitata* (Taylor et al. 1988), although this species is also known to lay aquatic eggs (Petranka 1998).

In Australia, many myobatrachid species in the genera *Pseudophryne* and *Geocrinia*, as well as foam-nesting *Heleioporus* (Limnodynastidae), lay their eggs on land in areas that later flood, and hatching may be delayed for weeks after hatching-competence if eggs are not submerged (Bradford and Seymour 1985; Barker et al. 1995). The most detailed studies have focused on *P. bibroni*. In this species,
embryos develop to hatching competence in 36 days, then slow metabolism and development to conserve energy, allowing them to survive as long as 120 days without hatching (Bradford and Seymour 1985). Boundary layers of water around flooded eggs reduce the oxygen supply which, in turn, stimulates hatching (Bradford and Seymour 1988). Phyllomedusine treefrogs lay eggs on vegetation above water, into which tadpoles fall upon hatching. Aerial incubation is obligate; embryos die if submerged in early development, for instance if the leaf to which they are attached falls into the water (Pyburn 1970). In all phyllomedusines tested to date, including five species of *Agalychnis*, *Pachymedusa dacnicolor*, and *Cruziohyla calcarifer*, flooding induces premature hatching (Gomez-Mestre et al. 2008b). Embryos become capable of hatching 28–36% before their modal spontaneous hatching age, depending on the species, and hatching-competent embryos do not drown. The capacity to hatch substantially prematurely and a strong hatching response to flooding appear to be ancestral phyllomedusine traits, dating back at least 34 my to their divergence from the aquatic-breeding pelodryadines (Gomez-Mestre et al. 2008b).

At least in *A. callidryas*, the red-eyed treefrog, and presumably in other phyllomedusines, hypoxia cues hatching of flooded eggs; embryos also hatch in hypoxic mixtures of gases (Warkentin 2002). *Agalychnis callidryas* eggs are packed closely together in their arboreal egg masses and, although eggs without exposure to air die, embryos develop normally in eggs with as little as 15% of their surface exposed. Perivitelline oxygen levels measured in the centers of eggs range from 0.5–16 kPa (2–60% air saturated) but, surprisingly, this does not affect development.

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or timing of hatching (Warkentin et al. 2005). Embryos maintain large external gills until hatching, whenever hatching occurs, and behaviorally position their gills near the air-egg surface, where oxygen is highest; indeed, they position themselves in oxygen gradients as soon as ciliary rotation develops, turning their developing head toward the air (Rogge and Warkentin 2008). Oxygen-sensitive behavior and delayed regression of the external gills both appear to be critical for normal synchronous development before hatching and for continued development in the egg after reaching hatching competence (Warkentin 2007). Moreover, presumably because embryos can experience positional hypoxia in eggs in air, their first response to flooding is to move. Embryos change position in the egg on average 16 times after flooding, extensively sampling the oxygen environment within their egg before hatching (K. Warkentin, unpublished data).

Hypoxia can accelerate hatching in aquatic eggs of amphibians (Figs. 1 and 2; Supplementary Table S1). Moderate hypoxia induces the myobatrachid *Crinia georgiana* to hatch earlier in both time and development; more extreme hypoxia slows development and delays the time of hatching, but induces hatching even earlier in development (Seymour et al. 2000). *Rana sphenoecephala* and *R. palustris* embryos hatch earlier in development and time under hypoxia (Mills and Barnhart 1999), and aquatic hypoxia also accelerates hatching of *Ambystoma texanum* eggs (Petranka et al. 1982). *Ambystoma maculatum* and *A. annulatum* showed slow development under hypoxia, with hatching delayed in time but at a developmentally earlier stage (Mills and Barnhart 1999).

Petranka et al. (1982) suggested that hypoxia may be a general trigger of hatching, and indeed hypoxia-induced or oxygen-inhibited hatching is phylogenetically widespread among amphibians (Fig. 1) and in other taxa (Gjullin et al. 1941; Miller 1992; Martin 1999; Czerkies et al. 2001; Mitterer 2008). The hypoxia-cued responses of terrestrial eggs of amphibians that wait for necessary flooding to hatch, of terrestrial eggs that hatch early in response to dangerous flooding, and of aquatic eggs that hatch developmentally earlier under hypoxia all appear mechanistically related. The broad periods of hatching competence and strong responses to hypoxia in terrestrial eggs may have evolved from similar responses of lesser magnitude in their aquatic ancestors. Data on embryos’ responses to hypoxia in additional species with aquatic eggs would be useful to assess the generality of these responses. Moreover, if hypoxia is a general trigger of hatching, it may be useful as a tool to map the onset of hatching competence across taxa.

Not only can terrestrial embryos of amphibians delay hatching and thereby avoid desiccation of the larvae, embryos in egg masses laid on vegetation above water may escape from drying eggs by accelerating hatching (Figs. 1 and 2; Supplementary Table S1). In the treefrog *Dendropsophus ebraccatus* dehydration frequently kills eggs, and embryos in drying clutches hatch 17% earlier, and more synchronously, than do those in well-hydrated egg masses (Touchon and Warkentin 2010; Touchon et al. 2011). Similarly in a glass frog, *Hyalinobatrachium fleishmanii*, in which paternal care seems important for keeping clutches hydrated during dry weather, removal of the parent causes clutches to hatch about 30% earlier and more synchronously (Delfia 2011). These species represent two independent origins of terrestrial eggs laid over water. In phylomedesines, another origin of a similar reproductive mode, *A. callidryas* eggs also appear to hatch earlier under dehydrating conditions, although the response is of lesser magnitude than is their response to flooding (K. Warkentin, personal observation). The specific cues mediating the responses of embryos to dehydration of eggs are unknown.

In addition to their direct effects on egg and hatching survival, abiotic factors can alter predator-prey interactions. Although hatching during low-risk periods in abiotic cycles that affect predation upon hatchlings is well documented in crabs (Christy, this volume) and fishes (Asoh and Yoshikawa 2002; Bradbury et al. 2004), the possible existence of such patterns of hatching in amphibians is largely untested. Diel timing of hatching may be generally important for species with cyclically active predators. For instance, visually foraging diurnal predators of larvae may select for hatching shortly after dark, which would allow hatchlings to disperse and hide during a period of relative safety. *Agalychnis callidryas* show such a pattern, which appears to improve their survival in bodies of water containing predatory fish (M. Hughey and K. Warkentin, unpublished data).

**Responses to predators and pathogens**

Hatching early can allow embryos to escape from predators and pathogens of eggs. Hatching later can allow hatchlings to develop more before facing predators upon larvae; it also reduces their duration of exposure to those predators during a period of high vulnerability. Responses of embryos to predators and pathogens were first discovered in the 1990s.
(Sih and Moore 1993; Warkentin 1995) and are now documented for many species of amphibians (Figs. 1 and 2; Supplementary Table S1).

**Terrestrial eggs**

For some amphibians hatching involves a change of habitat, as when hatchlings fall from arboreal egg clutches into bodies of water below. This physical separation of life-stages makes risks to eggs and risks to larvae discrete, facilitating the measurement of stage-specific selection. It also creates clear trade-offs between stage-specific risks that may often favor the evolution of plastic, environmentally cued hatching. Risk-cued early hatching has been studied most extensively in one such species, the red-eyed treefrog, Agalychnis callidryas embryos can hatch as much as 30% before the peak of spontaneous hatching in response to attacks by egg-eating snakes and wasps, infection by a pathogenic fungus, and infestation by fly larvae (Warkentin 1995; 2000, Warkentin et al. 2001; M. Hughey and K. Warkentin, unpublished data). Snake-induced hatching is a response to the physical disturbance of egg clutches during attacks, specifically to vibrational cues (Warkentin 2005). Embryos begin hatching within seconds (Warkentin et al. 2007) allowing about 80% of them to escape from the snake (Gomez-Mestre and Warkentin 2007). Escape success is similarly high in response to attacks by wasps, averaging 84% for fully hatch-competent embryos (Warkentin et al. 2006a). As with flooding, slower-acting fungus and fly larvae appear rarely, if ever, to kill hatch-competent embryos (Warkentin et al. 2001; Hughey 2011; Warkentin, personal observation).

We used a half-sibling breeding design to assess genetic variation in hatching-related traits of A. callidryas and found substantially more additive genetic variation in the timing of spontaneous hatching than in the onset of hatching competence (I. Gomez-Mestre and K. Warkentin, unpublished data). This suggests a history of directional selection eroding genetic variation against some developmental constraint. Decapsulated embryos are viable in pond water prior to hatching competence, and the earliest hatching is similarly timed with both hypoxia and physical disturbance, indicating that detection of cues is not the limiting factor. The constraint may involve development of the mechanism by which hatching occurs.

Unlike most amphibians that hatch as larvae, the phyllomedusines that have been examined to date lack externally visible hatching glands and there is no gradual weakening of the egg membrane or capsule prior to hatching (Nokhabatolfoogahai and Downie 2007; Cohen et al. 2011). High-speed video of hatching in A. callidryas has revealed that rupture of the egg membrane occurs near the embryo’s mouth and does not require contact with the rupture site; embryos then use vigorous movements to enlarge the hole and exit through it (Cohen et al. 2011). We hypothesize that the initial stage of hatching is enzymatic and that hatching glands occur in the buccal cavity, as they do in some fishes (Yamamoto et al. 1979; Cohen et al. 2011).

Snakes prey on the arboreal eggs of many phyllomedusines, and field data indicate similar rates of attack on A. spurrelli and A. callidryas clutches present concurrently at a pond (Gomez-Mestre and Warkentin 2007). Although responses to flooding are similarly strong and effective across all phyllomedusines tested, and snake-induced hatching can occur at similar time-points as hatching in response to flooding, the strength of the response to snake attack varies. Four species, A. callidryas, A. annae, A. moreletii, and Pachymedusa dacnicolor, show strong responses with about 80% escape success, while A. spurrelli and A. saltator embryos respond more weakly and suffer higher mortality (Gomez-Mestre et al. 2008b). Even at the modal hatching age, only 28% of A. spurrelli embryos escaped snake attacks. A phylogenetic analysis reveals that the strength of the response to snake attacks changed twice (Gomez-Mestre et al. 2008b). "Cruziohyla is the sister group to the rest of the phyllomedusines, and Cruziohyla calcarifer hatches readily in response to artificial mechanical disturbance. We suspect they would also respond strongly to snakes, and such responses may be ancestral and widespread in the clade (Gomez-Mestre et al. 2008b)."

Based on their response to flooding, A. spurrelli and A. saltator embryos clearly are capable of hatching early and of responding strongly to some cues. Thus, their mortality from snake attacks appear to be caused by lower responsiveness to the cues available in that context. The primary cue in snake-induced hatching is physical disturbance of egg clutches, or vibrations (Warkentin 2005). Most phyllomedusines, and all those known to respond strongly to snake attack, have highly gelatinous, jiggly clutches. The two with weaker responses to snakes have clutches with a derived, less gelatinous structure that moves less during attacks, reducing vibrational cues available to embryos (Gomez-Mestre et al. 2008b). The structure of egg clutches is probably generally important in mediating not only the immediate physical environment of embryos but also the cues to environmental conditions that are available to them.
Direct experimental tests of the responses of embryos to predators have been conducted in two additional lineages in which arboreal eggs have evolved. The African reed frog *Hyperolius spinigularis* accelerates hatching, in time and in development, in response to attacks by egg-eating frogs and infestation by egg-eating fly larvae (Vonesh 2005a). A congener, *H. cinnamomeoventris*, hatches at a smaller size from fly-infested clutches, and slightly but not significantly earlier in time (Vonesh 2000). The hylid *Dendropsophus ebraccatus* can hatch developmentally prematurely when attacked by ants, accelerating hatching by as much as 33%, but their ability to do so is severely compromised by sublethal desiccation (Touchon et al. 2011). These eggs can also be flooded or directly laid in water, where they are attacked by conspecific tadpoles. During tadpole attacks, embryos hatch as much as 67% prematurely, although their success in escaping attack improves developmentally (Touchon et al. 2011).

Predator-induced hatching probably occurs in terrestrial amphibian eggs of other species. In the direct-developing *Eleutherodactylus coqui* males often protect their eggs from predators, including flies, ants, and conspecifics, but sometimes abandon them. Simulated attack can induce hatching 19% prematurely, resulting in smaller, less developed hatchlings that have shorter legs and poorer performance in jumping than do full-term hatchlings (Buckley et al. 2005). In a glass frog, *Hyalinobatrachium pulvatum*, hatching begins and ends sooner in clutches with high mortality, including that from predators, although potential responses to different causes of egg mortality were not separated (Hawley 2006). The ranid *Limnonectes arathooni* lays eggs terrestrially on stream banks. Embryos were observed to hatch rapidly in response to physical disturbance during attempted collection of eggs, and tadpoles escaped by sliding down the bank to the water (Brown and Iskandar 2000). Additional anecdotal reports of apparent disturbance-induced hatching suggest that other terrestrial and arboreal amphibian embryos may show similar escape responses (e.g., Tilley 1972). Indeed, certain types of physical disturbance are probably good indicators of elevated risk for terrestrial eggs.

**Aquatic eggs**

The risks and opportunities facing aquatic embryos differ from those for species with terrestrial eggs and aquatic larvae, as do the challenges of those who study each group. First, where eggs and larvae share a habitat, predators are not necessarily stage-specific. When predators eat both stages, it is not clear if, or how, embryos should respond to them. Direct measurements of stage-specific or stage-biased foraging by predators and of the fitness effects of hatching at different ages or developmental stages are necessary to assess the adaptive value of hypothesized or demonstrated shifts in the timing of hatching. However, embryos can potentially acquire information about predators of both stages and might respond to either or both. Thus, bidirectional adaptive shifts in the timing of hatching could occur in response to predators of different stages. Second, water carries cues. Many aquatic animals, including embryos within eggs (Warkeintin, this volume), respond to water-borne chemicals indicating the presence or activity of predators (Kats and Dill 1998). Embryos might also assess mechanical cues, particularly in direct attacks, but this is relatively unexplored. If embryos respond to an indirect cue, such as a water-borne chemical, they have earlier warning of risk than if they rely on cues during direct attacks. However, the presence of a predator elsewhere in a pond, even a predator feeding on conspecific embryos, clearly poses less danger than does a predator currently attacking an egg clutch. Responses to indirect cues might, therefore, be weaker than those to direct cues.

There is clear evidence that aquatic amphibian embryos alter their timing of hatching in response to predators and pathogens of eggs and predators of larvae (Figs. 1 and 2; Supplementary Table S1). For instance, streamside salamanders, *Ambystoma barbouri*, can delay hatching in response to chemical cues from flatworms that prey on larvae but not on eggs, and the developmentally more advanced hatchlings are better able to escape from the flatworms (Sih and Moore 1993). These embryos also delay hatching by 7% in response to cues from sunfish; eggs are laid under rocks where they are protected from sunfish and more developed hatchlings may be able to better avoid drifting into pools with fish (Moore et al. 1996). Delayed hatching in response to cues from predators has also been documented for *Rana clamitans* and *R. temporaria* (8–11%, Laurila et al. 2002; Schalk et al. 2002; Ireland et al. 2007).

Accelerated hatching of aquatic eggs in response to cues from predators or pathogens occurs in a larger number of species (Supplementary Table S1 and Fig. 2). For instance, American toads, *Bufo americanus*, hatch as early as the tailbud stage (Gosner 1960 stage 17) in response to pathogenic water molds (Touchon et al. 2006). These early hatchlings are not yet capable of swimming, which requires
muscular movement. Nonetheless, exiting from the egg capsule via enzymatic digestion and slow ciliary movement allows them to escape from the oomycete hyphae (Gomez-Mestre et al. 2006). These embryos also accelerate hatching, but more moderately, in response to chemicals from crushed conspecific eggs, a putative cue of predation (Touchon et al. 2006). As in red-eyed treefrogs, the timing of hatching in threatened *B. americanus* eggs, in this case mold-infected, varies less across genotypes than does spontaneous timing of hatching (Gomez-Mestre et al. 2008a). The timing of development of the hatching gland in other toads suggests this may constrain the onset of competence to hatch (Yamasaki et al. 1990). Wood frogs, *Rana sylvatica*, embryos also hatch early in response to water mold, although their response is not as extreme as in the toads (Touchon et al. 2006). They show a greater acceleration of hatching when exposed to mosquitofish, which might be a predator of eggs or larvae, and a larger response to direct contact with the fish than to chemical cues alone (Smith and Fortune 2009). The best evidence for a potentially adaptive bidirectional shift in the timing of hatching is in green frogs, *R. clamitans*. Their embryos accelerate hatching in response to cues from an egg-eating leech and delay hatching in response to cues from a dragonfly that preys on tadpoles but not on eggs (Ireland et al. 2007).

In several studies, embryos have not shown predicted responses to chemicals from aquatic predators, but these results have multiple possible causes. For instance, *Rana temporaria* may not respond to cues from egg-eating leeches, *Haemopsis sanguisuga*, (Laurila et al. 2002) or may accelerate hatching ~5% (Capellán and Nicieza 2007; Capellán and Nicieza 2010). Given the magnitude of the effect, this discrepancy might represent differences in experimental power rather than actual differences in the responses between experiments. In various species, embryos have either not responded to cues from aeshnid nymphs (Laurila et al. 2002; Anderson and Petranka 2003; Johnson et al. 2003; Dibble et al. 2009), hatched earlier (Laurila et al. 2002; Capellán and Nicieza 2010), or hatched later (Ireland et al. 2007). In some cases, embryos may be unable to discriminate between cues from injured eggs and those from injured larvae, or between cues from different predators (Touchon et al. 2006; Capellán and Nicieza 2010), although clearly in other cases they do discriminate (Ireland et al. 2007). Moreover, embryos may respond more strongly to direct exposure to predators than to subsets of cues abstracted from the predator-prey interaction. *Rana sylvatica* accelerated hatching by 35 hours upon direct exposure to mosquitofish, by 15 hours with the fish behind a barrier in the same container, and not at all in response to chemical cues transferred from another container (Dibble et al. 2009; Smith and Fortune 2009).

Experimental results showing no response, or apparently inappropriate responses, by aquatic embryos to cues from predators might indicate maladaptive reaction norms. Alternatively, they might be due to inadequate cues or the hypothesized response might not actually confer a benefit. More information on the specific sensory cues and mechanisms mediating the responses of embryos to predators would be useful, as would direct measurements of the effect of the timing of hatching on survival. For instance, if hatchlings are inactive they may suffer little predation from movement-cued aeshnids, particularly in complex natural habitats with alternative prey available. Moreover, water chemistry can alter the persistence and perception of cues. Thus, laboratory demonstrations of cued responses can reveal the capabilities of embryos, but field studies will be necessary to assess their expression and value in nature. Comparative studies using the same methods across multiple species of embryos or predators will be particularly valuable in assessing responses. To effectively compare results across different studies, we will need to know more than just the statistical significance of shifts in the timing of hatching, or their magnitude in relation to an arbitrary experiment duration. Ideally, studies should report the magnitude of effects in both time and development, starting from oviposition. If the exact time of oviposition is unknown, even estimates of the length of time from oviposition to the start of experiments would help in interpreting the magnitude of responses. Moreover, grounding studies of hatching plasticity in quantitative data on the fates of eggs and hatchlings in nature would help reveal the strength of, and variation in, selective trade-offs that shape cued responses.

**The roles of parents**

Parental care has evolved multiple times in amphibians, changing the environment for embryos and in some cases also for posthatching stages. The quality of parental care varies and could affect the timing of hatching via responses of embryos to the quality of the environment within their egg. Embryos with better care might hatch later than those with poor or no care, as in *Eleutherodactylus coqui* (Buckley et al. 2005) and *Hyalinobatrachium fleishmanni*
within terrestrial eggs that wait for flooding to hatch (Fig. 1). There are at least six origins of embryos in lineages faced with similar environmental conditions (Junca 1998; Wells 2007). In other species there may be selection against spontaneous hatching. For instance, tadpoles might fall into phytotelmata with larger tadpoles that would eat them, become more difficult for their parents to locate, or be exposed to terrestrial predators from which their egg capsules protected them. Field observations of Ranitomeya imitator reveal that fathers use their hind limbs to manipulate eggs and cause hatching (Brown et al. 2008; Brown et al. 2010); it is not clear if fathers break open the eggs, if fathers stimulate the embryos to hatch themselves, or if both occur (J. Brown, personal communication). The role of parents in the timing of hatching deserves more attention, both in amphibian species that provide posthatching care and in those in which care is restricted to the egg stage.

Evolution and magnitude of environmental effects on the timing of hatching

Responses to the same or similar environmental factors are widely distributed across amphibians, suggesting convergent evolution of the responses of embryos in lineages faced with similar environmental conditions (Fig. 1). There are at least six origins of terrestrial eggs that wait for flooding to hatch (two within Ambystoma); flooding-induced hatching is widespread in the arboreal eggs of phylomedusines, and mechanistically related premature-hatching in response to hypoxia has been demonstrated in aquatic eggs in three families. Some sensitivity of the developmental timing of hatching to availability of oxygen may be ancestral in amphibians, providing a starting point from which larger or more specialized responses, or potentially even responses to other cues, could evolve.

Accelerated hatching in response to aquatic predators of eggs has been documented in four families and delayed hatching in response to predators of larvae in two families. Most of these responses appear to be mediated by chemical cues but the specific nature of the cues is unknown. Some components of a mechanism for chemically cued hatching may be shared ancestral traits, while others may be derived in the context of specific predator-prey interactions. Physical disturbance of aquatic eggs also plays a role in some cases (Smith and Fortune 2009; Touchon et al. 2011) but this has been better studied for terrestrial eggs. Responses of terrestrial eggs to predators have been demonstrated, or are hypothesized based on responses to simulated attack, in five different lineages with independent origins of terrestrial eggs. In many cases these responses are cued by physical disturbance of egg clutches. This could be a widespread mechanism for predator-induced hatching and merits more attention. Some level of responsiveness of embryos to physical disturbance could be ancestral, but it has likely been amplified and refined in particular lineages. Responses to physical disturbance may also be relevant in parentally induced hatching. Pathogens of eggs induce early hatching in members of four families, including in species with aquatic eggs and species with terrestrial eggs, but the mechanisms that cue hatching are unknown.

As well as the evidence for similar responses in multiple lineages, responses of embryos to multiple environmental factors have been documented within lineages and within species. Once mechanisms for plastic, cued hatching exist, it may require few evolutionary steps to link the response to additional cues (Gomez-Mestre et al. 2008b). The distribution of ECH in amphibians suggests that such responses are not difficult to evolve or change, and we might expect to find many more cases. At this time it is impossible to identify origins of plasticity or of responses to most types of cues because most species and many families have not been tested for cued or plastic hatching and we know too little about the underlying mechanisms. In a phylogenetic context, strong evidence for the absence of responses could add as much to our understanding as would evidence for responses. The exception, for which we can identify origins, is responses to specifically terrestrial factors. Presumably these evolved independently in different lineages after their origins of terrestrial eggs. Nonetheless, these responses may be derived from pre-existing traits of aquatic-breeding ancestors. In very few cases do we have clear, strong evidence for a lack of response to factors that have been demonstrated to matter in nature (but see Gomez-Mestre and Warkentin 2007; Gomez-Mestre et al. 2008b on Agalychnis spurrelli and A. saltator).

Thus, we should not consider the absence of evidence in particular areas to be evidence for the absence of environmentally cued hatching.

The magnitude of shifts in the timing of hatching, relative to the spontaneous or control embryonic
period, varies substantially (Fig. 2 and Supplementary Table S1). By far the longest delays occur in species that depend on unpredictable flooding to provide a suitable habitat for larvae. Moderate delays can also occur with sporadic emergence of normally aquatic eggs into air but, to date, only relatively small delays (7–11%) have been found in response to biotic factors. This contrasts strongly with the two-fold delay of hatching in snails exposed to cues from starved conspecifics (Voronezhskaya et al. 2004) and the even longer delays in parasites awaiting cues from a host (Whittington and Kearns, this volume). Extended environmentally cued delays in hatching, in amphibians and other taxa, appear to require reductions in development rate and metabolism (Bradford and Seymour 1985). Delays can also be caused directly by conditions that limit development (e.g., cold, hypoxia). In contrast, short cued delays result in slightly more developed hatchlings [2–8% longer, <1 Harrison (1969) or Gosner (1960) stage more advanced; Supplementary Table S1 and references therein]. This pattern suggests that amphibians may typically hatch close to the end of their developmental window of opportunity for hatching (Warkentin 2007, this volume).

Adaptive cued acceleration of the timing of hatching mediated by accelerated development in response to token stimuli appears to occur in birds and turtles (Vince 1968; Spencer and Janzen, this volume). In amphibians, however, there is no evidence for cued acceleration of development. Hatching earlier means hatching in a less developed state (Supplementary Table S1). I found 49 tests on 22 species, in 17 studies, that report significant accelerations of the timing of hatching, by 3–67%, and that also report hatchling size, developmental stage, or both. Of those, all but one found reductions in the size and/or stage of hatchlings [Supplementary Table S1; exception is the dehydration effect in (Touchon et al. 2011)]. Accelerations of hatching reduce the developmental stage of hatchlings up to 3.5 Gosner (1960) stages, but the greatest reduction in hatching stage to date (4.3 GS) occurs in conjunction with a delay in hatching under hypoxia (Seymour et al. 2000). Average reductions in hatching size range from 5–32% of total length. The greatest reduction in hatching size reported is 50% for some sibships of *Bufo americanus*, associated with a 56% acceleration (Gomez-Mestre et al. 2008a). Many amphibians appear to have considerable scope for developmentally and temporally accelerated hatching (Fig. 2, Supplementary Table S1).

The greatest acceleration of hatching, just after the onset of muscular response in *Dendropsophus ebraccatus*, may be partially mediated by attacking tadpoles physically disrupting the egg capsules (Touchon et al. 2011). Developmentally earlier hatching, at the tailbud stage, occurs in *Bufo americanus* in response to water mold hyphae that can penetrate egg capsules (Touchon et al. 2006). More information on the mechanisms of hatching is required to determine to what extent these early embryos play an active role in rupturing their capsules versus taking advantage of their enemies’ effects on the integrity of egg capsules; either way, however, they exit from the capsules themselves. Accelerations of 10–40% in the timing of hatching appear relatively common in response to a wide variety of direct abiotic and biotic threats to eggs (Fig. 2). In most cases these are clearly mediated by cued responses of embryos, not environmental effects on the integrity of the egg capsule.

Phyllomedusine embryos that respond immediately to acute direct threats, such as flooding and attack by predators, show a similar capacity for accelerating hatching in response to multiple threats. Responses to chronic conditions, such as levels of dissolved oxygen, or indirect cues, such as chemicals from predators, can vary in magnitude with the level of risk or constraint (Seymour et al. 2000; Johnson et al. 2003). Moreover, some embryos show greater acceleration of hatching in response to multimodal cues that include physical disturbance than they do to chemicals alone (Smith and Fortune 2009). Indeed, unlike responses to direct attack or to abiotic threats, responses to chemical cues alone are mostly small in magnitude (<11%; Fig. 2 and Supplementary Table S1). This is consistent with the lower risk posed by the mere presence of predators in a pond compared to the higher risk involved in a direct attack.

**Selective trade-offs favoring plasticity in hatching**

We know more about the existence of plastic, environmentally cued hatching in amphibians than we do about its adaptive value, which depends on variable trade-offs between selection on prehatching and posthatching stages. In some cases, these trade-offs seem obvious, as in the terrestrial eggs that wait for flooding to occur before they hatch. In the absence of a pond, high larval mortality selects against hatching, whereas the ability to feed and continue development favors hatching once a pond is present. Nonetheless, larvae of some amphibians, such as
**Pseudophryne bibroni**, can survive for days on wet soil, without free water (Geiser and Seymour 1989). In other species, hatchlings can survive extended periods on land as nonfeeding tadpoles in association with the remains of their gelatinous egg clutch or foam nest (Barker et al. 1995; Wells 2007); if this is the likely ancestral state, measurements of the relative benefits of delayed hatching versus delayed emergence from the nest would be worthwhile.

When predators or pathogens are directly attacking a clutch and killing eggs, or are highly likely to do so, the benefits of accelerating hatching also seem obvious. However, the efficacy of hatching as an escape mechanism must be measured. There is strong evidence that hatching allows escape from risks to embryos in multiple species with arboreal eggs and aquatic hatchlings (e.g., Gomez-Mestre et al. 2008b; Touchon et al. 2011). There is less evidence for this in aquatic eggs, but the stage-specificity of predators of eggs and the escape of hatchlings from pathogens of eggs has been demonstrated in some cases (Gomez-Mestre et al. 2006; Ireland et al. 2007) (Supplementary Table S1). Moreover, the rate at which natural enemies kill embryos will also affect the strength of selection they impose for accelerated hatching. The responses of embryos are congruent with variation in the rate of mortality in some cases. For instance, the growth rate of oomycetes increases with temperature, and wood frog embryos that typically develop in cold water show a smaller oomycete-induced acceleration of hatching than do toad embryos that develop in warmer water (Gomez-Mestre et al. 2006). Hatching-competent red-eyed treefrog embryos hatch rapidly when individually attacked by either wasps or snakes; however, embryos elsewhere in the same clutch are more likely to hatch during attacks by rapidly feeding snakes than in those by slowly foraging wasps (Warkentin et al. 2006a, 2007). The benefit of a predator-cued delay in hatching, to my knowledge, has only been shown in one case; streamside salamanders are better able to escape from flatworms if they are more developed at hatching (Sih and Moore 1993). Even for predators such as odonates that eat only larvae, not eggs, selection for later hatching will depend on how risk changes developmentally and accumulates over time; inactive early hatchlings might face relatively low risk (Skelly 1994).

For both cued accelerations and cued delays in hatching, we know less about the adaptive value of plasticity than we do about the value of induced traits. This is not surprising, given that the source of selection and of the cue are often the same, but to understand the adaptive value of plasticity, we need information on both sides of selective trade-offs (Travis 1994; Gotthard and Nylin 1995). If there is no source of opposing selection, the plasticity may be simply a means whereby an adaptive trait occurs. Moreover, we may be underestimating the occurrence or value of cued timing of hatching in cases where embryos use cues that are merely associated with risk or opportunity, such as environmental cycles (Christy, this volume; Warkentin, this volume), rather than cues directly generated by the agent of selection. Evidence to date suggests that costs of early hatching are likely to be strongest in the period immediately following hatching. For instance, early-hatched red-eyed treefrogs suffer higher mortality from all six aquatic predators we have tested. In most cases this appears as higher short-term predation rates (Warkentin 1995). In contrast, predation by movement-cued odonates increases as tadpoles develop but the greater duration of exposure of early hatchlings results in higher cumulative predation (Palmer et al. 2011; Willink et al. 2011). In all phyllomedusines tested, premature hatchlings are more vulnerable than are full-term hatchlings to predatory poeciliid fishes (Gomez-Mestre et al. 2008b). Biotic selective trade-offs might be more widespread, but relatively few have been demonstrated to date. For instance there is some evidence for a predation cost of oomycete-induced early hatching, but this is relatively weak, particularly for toads (Gomez-Mestre et al. 2006) and early hatching improves survival of *Hyperolius spinigularis* larvae (Vonesh 2005a).

The possibility of longer-term costs of hatching early has been examined in three anurans. In *H. spinigularis*, early hatchlings are smaller at metamorphosis and face higher risk of predation by spiders (Vonesh 2005b; Vonesh and Bolker 2005). In *Rana temporaria*, there are small but detectable effects of timing of hatching on the shape of metamorphs but no evidence that these affect performance or fitness. Larger shifts in the timing of hatching (Fig. 2) may be more likely to incur costs. We are assessing longer-term effects of the timing of hatching in *A. callidryas* and, so far, have found little effect on the traits of metamorphs; effects of the timing of hatching on early posthatching mortality are still evident at metamorphosis in some experiments but are swamped by later variation in others (Vonesh et al. 2011; J. Touchon et al., unpublished data).

**Specificity of cued responses**

The specificity of cues affects the ability of organisms to accurately match their phenotypic responses to...
environmental conditions. Accurate matching requires both differences between properties of the salient stimulus and background conditions the animal is likely to experience and the sensory, and potentially cognitive, capacity to discriminate those differences. There are three types of stimuli that appear common in environmentally cued hatching of amphibians: hypoxia, chemical cues, and physical disturbance. Other kinds of stimuli, such as light, may also be relevant.

Hypoxia stimulates or accelerates hatching of flooded terrestrial eggs, as well as of aquatic eggs, in multiple contexts (Figs. 1 and 2; Supplementary Table S1). Where these responses have been studied, they appear to require a period of sustained hypoxia, or an oxygen level well below that which begins to limit embryonic metabolism; hatching-competent embryos tolerate moderate metabolic suppression without hatching (Bradford and Seymour 1988; Seymour et al. 2000; Rogge and Warkentin 2008). The stringency of this condition likely limits the incidence of hatching in response to brief, transient flooding.

The distinctiveness of chemical cues from stage-specific predators, or embryos’ ability to discriminate them, appears to vary. In some cases embryos do discriminate, responding differently to predators of eggs than to those of larvae (Fig. 2 and Supplementary Table S1). In others they seem not to. Several hypothetically maladaptive cued shifts in the timing of hatching involve small accelerations of hatching in response to chemical cues from odonates that were fed tadpoles, or simply to cues from crushed tadpoles (Laurila et al. 2002; Touchon et al. 2006; Capellán and Nicieza 2010). Embryos may be unable to chemically distinguish injured hatchlings from embryos. When maladaptive responses are small in magnitude, selection against them may be relatively weak, and costs of these putative mistakes have not been measured. However, the selective cost of phenotypic errors elicited by non-specific cues might also limit the evolution of stronger responses.

Physical disturbance of eggs, as occurs during attacks by predators, cues hatching of terrestrial eggs in several amphibian lineages (Fig. 1 and Supplementary Table S1). Physical disturbance can also accelerate hatching of aquatic eggs, and this mechanism may play a role in parentally induced hatching (Supplementary Table S1). Anecdotally, there is a perception among herpetologists that small accelerations of hatching commonly occur in response to physical disturbance of eggs; i.e., eggs near the stage of spontaneous hatching often hatch during collection. In some cases, this may reflect the effect of mechanical stress on weakened egg membranes during an extended intrinsic hatching process, rather than a cued response to disturbance. Hatching cued by physical disturbance has also been considered to be nonspecific, i.e., a general response to any sort of disturbance (e.g., Savage 2002, p. 282). This may be true in some cases but, to my knowledge, the specificity of embryos’ responses to physical disturbance has only been tested for red-eyed treefrogs.

We have recorded vibrations from *A. callidryas* egg clutches in multiple contexts and conducted a series of vibration-playback experiments to examine embryos’ responses to different properties of physical disturbance patterns (Warkentin and Caldwell 2009). Embryos face a challenge in discriminating cues because vibrations caused by rainstorms, a common benign disturbance, overlap with those caused by snake attacks for every vibration property we have measured. This means there is no simple, fast way to accurately distinguish these different sources of vibration. Nonetheless, the vibration-cued early hatching of *A. callidryas* is a very specific response, and most vibrations we have played to eggs elicit little or no premature hatching. Embryos combine information from multiple properties of the vibrations to achieve this specificity. Durations of and intervals between vibrations affect hatching, individually and interactively; low frequencies are stimulatory and high frequencies are inhibitory; and some property of the onset of vibrations also affects embryos’ responses (Warkentin et al. 2006b; Caldwell et al. 2009; 2010). In addition, the hatching response increases more rapidly with amplitude of the stimulus for vibrations generated by snakes than for vibrations caused by rain (Caldwell 2010). These properties of the cues are nonredundant; each adds information and narrows the range of stimuli that elicit hatching, thereby reducing the chance of false alarms. Moreover, embryos sample a period of vibrations before hatching, and they vary their sampling period with the rate at which information relevant to assessment of risk accrues (Warkentin et al. 2007).

The highly specific vibration-cued hatching response of *A. callidryas* demonstrates that embryos can be capable of complex, multifaceted assessment of their environment. For many embryos, physical disturbance may be a good general indicator of risk. The incidence of benign disturbance, and thus the likelihood of false alarms from a general response to disturbance, likely varies substantially with oviposition site and with the existence and type of parental care. Even if disturbance-cued hatching was,
ancestrally, a nonspecific response of amphibian embryos, greater specificity may well have evolved in additional lineages in which selective trade-offs across hatching are strong and the potential for false alarms in response to benign disturbance is high. If hatching responses to physical disturbance in other species are mediated by vibrational cues, as in *A. callidryas*, they will be amenable to similar experimental analysis and tests of specificity using playbacks.

**Future directions**

There are several areas where more information would be valuable for constructing a more complete and nuanced understanding of the evolution and function of plasticity of hatching in amphibians.

1. The starting point for assessing environmentally cued hatching, in most cases, is measuring the existence and direction of responses. To compare across taxa, information on the magnitude of shifts, both in time and in development, relative to a standard, is necessary. The most feasible standard is the embryonic period of control embryos that hatch spontaneously; embryos that wait for a cue to hatch could be transferred to conditions permissive of hatching prior to hatching competence. A potentially better set of comparative standards, although more challenging to assess, includes the onset of hatching competence and the maximal duration of the embryonic stage, i.e., the limits of the plastic hatching period (Gomez-Mestre et al. 2008b; Warkentin, this volume).

2. To assess the adaptive value of plasticity in hatching, we need information on the effectiveness of cued responses, or the fitness benefit they confer, given the inducing condition. We also need information on the trade-offs or costs of the response that select for plasticity and the magnitude and pattern of environmental heterogeneity for factors involved in selective trade-offs.

3. In most cases we know very little about cues beyond, perhaps, the sensory modality through which they are perceived. More information on the nature of cues, their specificity, and the sensory physiology underlying environmental assessment by embryos might substantially alter our perspective on the evolution of cued hatching. Moreover, in the absence of detailed information on cues, we should not assume that responses to subsets of cues fully represent the responses of animals in nature.

4. The speed of responses sets the lag time that can limit the value of cued responses. For instance, the slow hatching response of toad embryos to water mold would not save them from a snake attack. Mechanisms of hatching determine the minimum lag time in accelerated hatching and may constrain the maximum possible acceleration, the lead time necessary to delay hatching, and the maximum possible delay in hatching. Our current knowledge of the mechanisms of hatching in amphibians (e.g., Salthe 1963; Duellman and Trueb 1986; Yamasaki et al. 1990; Drysdale and Elinson 1991; Nokhbatolfoghahai and Downie 2007) almost certainly underestimates the diversity that exists, and reveals nothing about how these mechanisms mediate shifts in the timing of hatching. This is an area ripe for investigation.

5. As with other life-history switch points, shifts in the timing of hatching could confer fitness benefits in the context of multiple stage-specific risks and opportunities (Gomez-Mestre et al. 2008b). Selective trade-offs may act synergistically to favor increased plasticity, or plasticity that evolved in response to one selective factor may be co-opted to function in the context of another. Variation in the magnitude of responses to different factors, or in the proportion of cued embryos that exhibit them (i.e., response strength) is relevant in two contexts. It should covary with the strength of selective trade-offs, and it may also reveal components of the underlying mechanisms linking cues with responses. Thus assessing responses of embryos to multiple risks is worthwhile.

6. The robustness of cued hatching responses, or their consistency across other conditions, appears to vary. How likely is it than an adaptive cued response to one factor, such as the early hatching of *D. ebraccatus* embryos to escape from predatory ants, can be ablated by a change in another environmental variable? This may be particularly relevant in nature where environmental conditions, such as changing weather patterns, affect the structure of egg clutches or capsules in a way that hinders or facilitates hatching (Touchon et al. 2011) or if water chemistry affects the persistence or perception of chemical cues (Lürling and Scheffer 2007). It may also explain inconsistent results across experiments that vary slightly in their
methods, making species with robust responses more tractable for studies of mechanisms underlying cued responses.

(7) Knowledge of what constrains both the range of hatching phenotypes and the types of cues to which embryos respond would also substantially improve our understanding of the plasticity of hatching. This includes mechanisms underlying the hatching process, traits determining the onset of hatching competence, traits determining how long embryos can survive and develop in the egg including their capacity for periods of reduced metabolism and slowed or static development, and the sensory physiology of environmental assessment (Warkentin, this volume).

(8) Environmentally cued hatching likely occurs and may be important both in contexts and in lineages in which it has not yet been studied. In other cases we have an indication that such plasticity exists but know little else. Promising areas for investigation include: species with parental care, in which parents could induce hatching or care could shift the optimal time or stage of hatching; additional lineages in which eggs and larvae occur in discrete habitats, since this creates opportunities for strong selective trade-offs; responses of embryos to physical disturbance, the specificity and ecological role of which we may have underestimated; and hatching timed with environmental correlates of risk, which has received little attention despite its potential ecological importance and likely experimental tractability (Christy, this volume).

(9) To date there has been only one comparative analysis of the evolution of environmentally cued hatching within a group of closely related amphibians (Gomez-Mestre et al. 2008b). Several clades appear promising for such analyses. In particular, investigations of clades in which a diversity of potentially related responses are known may elucidate evolutionary transitions in plasticity and its underlying mechanisms. For instance, both myobatrachids and ambystomatids offer opportunities to investigate the evolution of extreme delays in hatching by embryos waiting to be flooded, and the relationship of hypoxia-cued hatching in this context to the hypoxia-accelerated hatching of aquatic embryos.

There is both great depth and breadth in the research possibilities offered by environmentally cued hatching. Embryos and hatchlings are more abundant and, for many species, more tractable as subjects for study than are later life-stages. They merit study in their own right, as an essential part of animal life cycles. They also offer excellent opportunities for research on many questions that are relevant for other life-stages, particularly for integrative studies of mechanisms, evolution, and ecology of a critical life-history transition point.

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Supplementary Data
Supplementary data are available at ICB online.

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Table S1. Environmentally cued shifts in hatching of amphibians in response to abiotic and biotic factors affecting eggs and post-hatching stages.

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<th>Development at hatching (rate before)</th>
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<tr>
<td><em>Ambystoma opacum</em></td>
<td>Air exposure, then flooding</td>
<td>Hypoxia after 2 wk or more</td>
<td>Uncued</td>
<td>+86 d</td>
<td>+614% (slow)</td>
<td>(slow)</td>
</tr>
<tr>
<td><em>Ambystoma cingulatum</em></td>
<td>Air exposure</td>
<td>Flooding 2 wk</td>
<td>Change</td>
<td>+12 wk</td>
<td>+500% (slow)</td>
<td>(slow)</td>
</tr>
<tr>
<td><em>Ambystoma gracile</em></td>
<td>Air exposure</td>
<td>Flooding 30-60 d</td>
<td>Change</td>
<td>+11 d</td>
<td>+37% similar</td>
<td>similar</td>
</tr>
<tr>
<td><em>Ambystoma maculatum</em></td>
<td>Hypoxic water</td>
<td>~21 d</td>
<td>Change</td>
<td>+9 d</td>
<td>+43% ~3 HS (slow)</td>
<td>~3 HS (slow)</td>
</tr>
<tr>
<td><em>Ambystoma annulatum</em></td>
<td>Hypoxic water</td>
<td>~28 d</td>
<td>Change</td>
<td>+6 d</td>
<td>+21% ~2 HS (slow)</td>
<td>~2 HS (slow)</td>
</tr>
<tr>
<td><em>Ambystoma texanum</em></td>
<td>Hypoxic water</td>
<td>Hypoxia</td>
<td>Change</td>
<td>~</td>
<td>~</td>
<td>~</td>
</tr>
<tr>
<td><em>Eurycea quadridigitata</em></td>
<td>Air exposure</td>
<td>Flooding</td>
<td>Change</td>
<td>~</td>
<td>~</td>
<td>~</td>
</tr>
<tr>
<td><em>Amphiuma means</em></td>
<td>Air exposure</td>
<td>Flooding</td>
<td>Change</td>
<td>+93 d</td>
<td>+219% TL</td>
<td>+9% TL</td>
</tr>
<tr>
<td><em>Pseudophryne bibroni</em></td>
<td>Air exposure</td>
<td>Flooding/hypoxia 39 d</td>
<td>Change</td>
<td>+101 d</td>
<td>+259% more (slow)</td>
<td>+259% more (slow)</td>
</tr>
<tr>
<td><em>Crinia georgiana</em></td>
<td>Hypoxic water</td>
<td>5 vs. 21 kPa</td>
<td>Change</td>
<td>~12 d</td>
<td>~9% ~1 GS (=)</td>
<td>~1 GS (=)</td>
</tr>
<tr>
<td><em>Crinia georgiana</em></td>
<td>Hypoxic water</td>
<td>2 vs. 21 kPa</td>
<td>Change</td>
<td>~12 d</td>
<td>+0.8 d</td>
<td>+6% ~4.3 GS</td>
</tr>
<tr>
<td><em>Agalychnis callidryas</em></td>
<td>Flooding 5</td>
<td>Flooding/hypoxia 172 h</td>
<td>Change</td>
<td>~54 h</td>
<td>~30% ~19% TL</td>
<td>~30% ~19% TL</td>
</tr>
<tr>
<td><em>Agalychnis annae</em></td>
<td>Flooding 5</td>
<td>Flooding 188 h</td>
<td>Change</td>
<td>~47 h</td>
<td>~28% ~14% TL</td>
<td>~28% ~14% TL</td>
</tr>
<tr>
<td><em>Agalychnis moreletii</em></td>
<td>Flooding 5</td>
<td>Flooding 260 h</td>
<td>Change</td>
<td>~96 h</td>
<td>~36% ~18% TL</td>
<td>~36% ~18% TL</td>
</tr>
<tr>
<td><em>Agalychnis saltator</em></td>
<td>Flooding 5</td>
<td>Flooding 140 h</td>
<td>Change</td>
<td>~48 h</td>
<td>~35% ~27% TL</td>
<td>~35% ~27% TL</td>
</tr>
<tr>
<td><em>Agalychnis spurrelli</em></td>
<td>Flooding 5</td>
<td>Flooding 148 h</td>
<td>Change</td>
<td>~49 h</td>
<td>~33% ~13% TL</td>
<td>~33% ~13% TL</td>
</tr>
<tr>
<td><em>Pachymedusa dacnicolor</em></td>
<td>Flooding 5</td>
<td>Flooding 216 h</td>
<td>Change</td>
<td>~76 h</td>
<td>~32% ~21% TL</td>
<td>~32% ~21% TL</td>
</tr>
<tr>
<td><em>Cruziohyla calcarifer</em></td>
<td>Flooding 5</td>
<td>Flooding 280 h</td>
<td>Change</td>
<td>~75 h</td>
<td>~29% less</td>
<td>~29% less</td>
</tr>
<tr>
<td><em>Rana sphenoecephala</em></td>
<td>Hypoxic water</td>
<td>2.6 vs. 16.9 kPa</td>
<td>Change</td>
<td>~11 d</td>
<td>~36 d</td>
<td>~32% ~2-3 GS (=)</td>
</tr>
<tr>
<td><em>Rana palustris</em></td>
<td>Hypoxic water</td>
<td>2.6 vs. 16.9 kPa</td>
<td>Change</td>
<td>~11.5 d</td>
<td>~2.5 d</td>
<td>~22% ~2-3 GS (=)</td>
</tr>
</tbody>
</table>

1 Primary or obligate incubation period for species that wait for a cue to hatch, spontaneous hatching timing for species induced to hatch early, control incubation period plus estimated starting age for experiments; varies with temperature and some estimates are rough.

2 Development at hatching incorporates information on size and morphology. Development rate before hatching is assessed across embryonic period for manipulations of oxygen level in water but after obligate incubation period for species waiting for a hatching cue. Developmental stage information is difference in Harrison (1969) Stages (HS) for salamanders and Gosner (1960) Stages (GS) for anurans. Size information is % difference in total length (TL).

3 Eggs laid terrestrially in flood-prone areas, wait to hatch until flooded.

4 Eggs laid aquatically, can be exposed by drying of ponds.

5 Terrestrial incubation normal, nest position relative to water level at oviposition unknown.

6 Arboreal eggs above water risk flooding if leaf falls or water rises; eggs die if flooded early in development.
### B. Responses to abiotic environmental conditions: Risk of desiccation

<table>
<thead>
<tr>
<th>Species</th>
<th>Environmental factor</th>
<th>Specific cues, treatments, conditions</th>
<th>Hatching timing</th>
<th>Relative change</th>
<th>Development at hatching</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dendropsophus ebraccatus</em></td>
<td>Dehydration</td>
<td>Dehydration</td>
<td>95 h</td>
<td>– 16 h</td>
<td>– 17%</td>
<td>Touchon et al. 2011</td>
</tr>
<tr>
<td><em>Hyalinobatrachium fleischmanni</em></td>
<td>Dehydration</td>
<td>Dry weather + no paternal care</td>
<td>19 d</td>
<td>– 6 d</td>
<td>– 31%</td>
<td>Delia 2011</td>
</tr>
</tbody>
</table>

### C. Responses to egg pathogens (infection of egg clutch)

<table>
<thead>
<tr>
<th>Species</th>
<th>Environmental factor</th>
<th>Specific cues, treatments, conditions</th>
<th>Hatching timing</th>
<th>Relative change</th>
<th>Development at hatching</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ambystoma maculatum</em></td>
<td>Oomycete infection</td>
<td><em>Saprolegnia, Achlya</em></td>
<td>34 d</td>
<td>– 8 d</td>
<td>– 24%</td>
<td>Gomez-Mestre et al. 2006</td>
</tr>
<tr>
<td><em>Bufo americanus</em></td>
<td>Oomycete infection</td>
<td><em>Saprolegnia, Achlya</em></td>
<td>14 d</td>
<td>– 5 d</td>
<td>– 36%</td>
<td>Gomez-Mestre et al. 2006</td>
</tr>
<tr>
<td><em>Bufo americanus</em></td>
<td>Oomycete infection</td>
<td><em>Saprolegnia, Achlya</em></td>
<td>18.6 d</td>
<td>– 8.2 d</td>
<td>– 44%</td>
<td>Touchon et al. 2006</td>
</tr>
<tr>
<td><em>Agalychnis callidryas</em></td>
<td>Fungus infection</td>
<td>Dothideales</td>
<td>6 d</td>
<td>– 1 d(^7)</td>
<td>– 17%</td>
<td>Warkentin 2001, 2005</td>
</tr>
<tr>
<td><em>Rana sylvatica</em></td>
<td>Oomycete infection</td>
<td><em>Saprolegnia, Achlya</em></td>
<td>20 d</td>
<td>– 2.6</td>
<td>– 13%</td>
<td>Gomez-Mestre et al. 2006</td>
</tr>
<tr>
<td><em>Bufo americanus</em></td>
<td>Oomycete infection</td>
<td><em>Saprolegnia, Achlya</em></td>
<td>12.7 d</td>
<td>– 2.5</td>
<td>– 19%</td>
<td>Touchon et al. 2006</td>
</tr>
<tr>
<td><em>Agalychnis callidryas</em></td>
<td>Wasp attack</td>
<td>Physical disturbance</td>
<td>6.8 d</td>
<td>– 2.3 d(^7)</td>
<td>– 34%</td>
<td>Warkentin 2000, 2006</td>
</tr>
<tr>
<td><em>Agalychnis annae</em></td>
<td>Snake attack</td>
<td>Physical disturbance</td>
<td>188 h</td>
<td>– 47 h</td>
<td>– 28%</td>
<td>Gomez-Mestre et al. 2008</td>
</tr>
<tr>
<td><em>Agalychnis moreletii</em></td>
<td>Snake attack</td>
<td>Physical disturbance</td>
<td>260 h</td>
<td>– 96 h</td>
<td>– 36%</td>
<td>Gomez-Mestre et al. 2008</td>
</tr>
<tr>
<td><em>Agalychnis saltator</em></td>
<td>Snake attack</td>
<td>Physical disturbance</td>
<td>140 h</td>
<td>– 48 h</td>
<td>– 35%</td>
<td>Gomez-Mestre et al. 2008</td>
</tr>
<tr>
<td><em>Agalychnis spurrelli</em></td>
<td>Snake attack</td>
<td>Physical disturbance</td>
<td>148 h</td>
<td>– 49 h</td>
<td>– 33%</td>
<td>Gomez-Mestre et al. 2008</td>
</tr>
<tr>
<td><em>Pachymedusa dacnicolor</em></td>
<td>Snake attack</td>
<td>Physical disturbance</td>
<td>216 h</td>
<td>– 76 h</td>
<td>– 32%</td>
<td>Gomez-Mestre et al. 2008</td>
</tr>
<tr>
<td><em>Cruziohyla calcarifer</em></td>
<td>Simulated attack</td>
<td>Physical disturbance</td>
<td>280 h</td>
<td>– 75 h</td>
<td>– 29%</td>
<td>Gomez-Mestre et al. 2008</td>
</tr>
<tr>
<td><em>Hyperolius cinamomeoventris</em></td>
<td>Fly larvae</td>
<td>Infestation</td>
<td>14.3 d</td>
<td>– 0.8 d</td>
<td>– 6% ns</td>
<td>Vonesh 2000</td>
</tr>
<tr>
<td><em>Hyperolius spinigularis</em></td>
<td>Fly larvae</td>
<td>Infestation</td>
<td>10 d</td>
<td>– 4 d</td>
<td>– 40%</td>
<td>Vonesh 2005</td>
</tr>
<tr>
<td><em>Hyperolius spinigularis</em></td>
<td>Frog (<em>Afrixalus</em>)</td>
<td>Direct predation</td>
<td>10 d</td>
<td>– 2.6 d</td>
<td>– 26%</td>
<td>Vonesh 2005</td>
</tr>
<tr>
<td><em>Limnonectes arathooni</em></td>
<td>Simulated attack</td>
<td>Physical disturbance</td>
<td>rapid response to attempted collection</td>
<td></td>
<td></td>
<td>Brown &amp; Iskandar 2000</td>
</tr>
</tbody>
</table>

\(^7\) Fungus-infected *A. callidryas* hatch gradually; acceleration is relative to overall pattern for uninfected clutches. Timing of hatching in predator attacks reflects attack timing; data indicate onset of responsiveness. Uncued timing indicates peak of spontaneous hatching.

\(^8\) Townsend and Stewart (1985) Stages (TSS).
<table>
<thead>
<tr>
<th>Species</th>
<th>Environmental factor</th>
<th>Specific cues, treatments, conditions</th>
<th>Hatching timing</th>
<th>Rel. change</th>
<th>Development at hatching</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. Responses of terrestrial eggs to physical manipulation by parent</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ranitomeya imitator</em></td>
<td>Paternal male</td>
<td>Physical disturbance</td>
<td>hatching mediated/induced to transport tadpole</td>
<td>more</td>
<td></td>
<td>Brown et al. 2010</td>
</tr>
<tr>
<td><em>Ambystoma barbouri</em></td>
<td>LP flatworm</td>
<td>Direct contact, caged</td>
<td>~ 58 d</td>
<td>+</td>
<td>7%</td>
<td>+0.7 HS, 2% TL</td>
</tr>
<tr>
<td><em>Ambystoma barbouri</em></td>
<td>LP sunfish <em>Lepomis</em></td>
<td>Caged unfed</td>
<td>~ 36 d</td>
<td>none</td>
<td>0%</td>
<td>same</td>
</tr>
<tr>
<td><em>Ambystoma maculatum</em></td>
<td>LP dragonfly <em>Anax junius</em></td>
<td>Caged L-fed, unfed</td>
<td>~ 36 d</td>
<td>none</td>
<td>0%</td>
<td>-2% TL</td>
</tr>
<tr>
<td><em>Ambystoma maculatum</em></td>
<td>EP caddisfly</td>
<td>Direct exposure</td>
<td>~ 36 d</td>
<td>- 2 d</td>
<td>- 6%</td>
<td>less</td>
</tr>
<tr>
<td><em>Ambystoma maculatum</em></td>
<td>LP <em>Ambystoma opacum</em></td>
<td>Caged L-fed</td>
<td>~ 36 d</td>
<td>none</td>
<td>0%</td>
<td>same</td>
</tr>
<tr>
<td><em>Triturus helveticus</em></td>
<td>LP trout <em>Salmo trutta</em></td>
<td>Unfed pred. chem.</td>
<td>19.5 d</td>
<td>none</td>
<td>0%</td>
<td>-5% TL</td>
</tr>
<tr>
<td><em>Triturus alpestris</em></td>
<td>LP trout <em>Salmo trutta</em></td>
<td>Unfed pred. chem.</td>
<td>21.5 d</td>
<td>none</td>
<td>0%</td>
<td>-7% TL</td>
</tr>
<tr>
<td><em>Triturus boscai</em></td>
<td>LP trout <em>Salmo trutta</em></td>
<td>Unfed pred. chem.</td>
<td>31 d</td>
<td>none</td>
<td>0%</td>
<td>-7% TL</td>
</tr>
<tr>
<td><em>Triturus marmoratus</em></td>
<td>LP trout <em>Salmo trutta</em></td>
<td>Unfed pred. chem.</td>
<td>25.5 d</td>
<td>1 d</td>
<td>4% ns</td>
<td>-7% TL</td>
</tr>
<tr>
<td><em>Bufo americanus</em></td>
<td>Simulated EP–conspecific</td>
<td>Crushed E chem.</td>
<td>17.2 d</td>
<td>- 2.6 d</td>
<td>- 15%</td>
<td>less</td>
</tr>
<tr>
<td><em>Bufo americanus</em></td>
<td>Simulated LP–conspecific</td>
<td>Crushed L chem.</td>
<td>17.2 d</td>
<td>- 2.6 d</td>
<td>- 15%</td>
<td>less</td>
</tr>
<tr>
<td><em>Bufo americanus</em></td>
<td>Simulated EP–<em>Rana</em></td>
<td>Crushed E chem.</td>
<td>17.2 d</td>
<td>- 2.6 d</td>
<td>- 15%</td>
<td>less</td>
</tr>
<tr>
<td><em>Dendropsophus</em></td>
<td>Tadpole <em>D. ebraccatus</em></td>
<td>Physical disturbance</td>
<td>98 h</td>
<td>- 66 h</td>
<td>- 67%</td>
<td>-2.3 GS</td>
</tr>
<tr>
<td><em>Pseudacris regilla</em></td>
<td>EP leech <em>Deserobdella</em></td>
<td>Direct contact</td>
<td>~ 10 d</td>
<td>- 12 h</td>
<td>- 5%</td>
<td>-0.4 GS</td>
</tr>
<tr>
<td><em>Pseudacris regilla</em></td>
<td>EP leech <em>Deserobdella</em></td>
<td>Caged E-fed</td>
<td>~ 10 d</td>
<td>- 14 h</td>
<td>- 6%</td>
<td>-0.4 GS</td>
</tr>
<tr>
<td><em>Pseudacris regilla</em></td>
<td>Simulated egg predation</td>
<td>Crushed E chem.</td>
<td>~ 10 d</td>
<td>- 10 h</td>
<td>- 4%</td>
<td>-0.3 GS</td>
</tr>
<tr>
<td><em>Pseudacris regilla</em></td>
<td>Non-predatory earthworm</td>
<td>Direct contact</td>
<td>~ 10 d</td>
<td>- 13 h</td>
<td>- 5%</td>
<td>-0.4 GS</td>
</tr>
<tr>
<td><em>Pseudacris regilla</em></td>
<td>Non-predatory earthworm</td>
<td>Caged earthworm</td>
<td>~ 10 d</td>
<td>none</td>
<td>0%</td>
<td>same</td>
</tr>
<tr>
<td><em>Rana cascadae</em></td>
<td>EP leech <em>Deserobdella</em></td>
<td>Caged E-fed</td>
<td>~ 9 d</td>
<td>- 8 h</td>
<td>- 4%</td>
<td>less</td>
</tr>
<tr>
<td><em>Rana cascadae</em></td>
<td>Simulated egg predation</td>
<td>Crushed E chem.</td>
<td>~ 9 d</td>
<td>none</td>
<td>0%</td>
<td>same</td>
</tr>
</tbody>
</table>

9Stage at greater risk is specified for known egg predators (EP) and larval predators (LP); some predators are known or thought to eat both stages (E/LP), others may also.

10Caged predators were separated from embryos by a physical barrier, within the same container of water, and fed eggs (E), larvae (L) or unfed. For chemical cues, predators were held fed or unfed or eggs or larvae were crushed in a separate container and water was transferred to the container with test embryos.
<table>
<thead>
<tr>
<th>Species</th>
<th>Environmental factor $^b$</th>
<th>Specific cues, treatments, conditions $^{10}$</th>
<th>Hatching timing</th>
<th>Rel. change</th>
<th>Development at hatching</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Rana clamitans</em></td>
<td>LP dragonfly <em>Aeschna</em></td>
<td>Caged L-fed</td>
<td>~ 136 h</td>
<td>+ 12 h</td>
<td>+ 9%</td>
<td>Ireland et al. 2007</td>
</tr>
<tr>
<td><em>Rana clamitans</em></td>
<td>EP leech <em>Nepheleis</em></td>
<td>Caged E-fed</td>
<td>~ 136 h</td>
<td>− 15 h</td>
<td>− 11%</td>
<td>Ireland et al. 2007</td>
</tr>
<tr>
<td><em>Rana sylvatica</em></td>
<td>E/LP leech <em>Macrobdella</em></td>
<td>Caged unfed</td>
<td>4.5 d</td>
<td>+ 0.5 d</td>
<td>+ 11%</td>
<td>Schalk et al. 2002</td>
</tr>
<tr>
<td><em>Rana sphenoecephala</em></td>
<td>EP crayfish <em>Procambarus</em></td>
<td>Caged unfed</td>
<td>~ 83 h</td>
<td>− 11 h</td>
<td>− 13%</td>
<td>Johnson et al. 2003</td>
</tr>
<tr>
<td><em>Rana sphenoecephala</em></td>
<td>EP dytiscid larva <em>Cibister</em></td>
<td>Caged unfed</td>
<td>~ 83 h</td>
<td>− 5 h</td>
<td>− 6%</td>
<td>Johnson et al. 2003</td>
</tr>
<tr>
<td><em>Rana sylvatica</em></td>
<td>LP dragonfly <em>Anax jnunis</em></td>
<td>Caged L-fed, unfed</td>
<td>none</td>
<td>0%</td>
<td>same</td>
<td>Smith &amp; Fortune 2009</td>
</tr>
<tr>
<td><em>Rana arvalis</em>, Uppland</td>
<td>E/LP mosquitofish</td>
<td>Direct contact</td>
<td>~ 118 h</td>
<td>− 35 h</td>
<td>− 30%</td>
<td>Laurila et al. 2002</td>
</tr>
<tr>
<td><em>Rana arvalis</em>, Uppland</td>
<td>LP stickleback <em>Gasterosteus aculeatus</em></td>
<td>Caged L-fed</td>
<td>8.2 d</td>
<td>− 0.2 d</td>
<td>− 3%</td>
<td>Laurila et al. 2002</td>
</tr>
<tr>
<td><em>Rana arvalis</em>, Gotland</td>
<td>LP dragonfly <em>Aeschna</em> sp.</td>
<td>Caged L-fed</td>
<td>8.2 d</td>
<td>− 0.4 d</td>
<td>− 5%</td>
<td>Laurila et al. 2002</td>
</tr>
<tr>
<td><em>Rana arvalis</em>, Gotland</td>
<td>EP leech <em>Haemopis sanguineae</em></td>
<td>Caged E-fed</td>
<td>8.2 d</td>
<td>− 0.4 d</td>
<td>− 5%</td>
<td>Laurila et al. 2002</td>
</tr>
<tr>
<td><em>Rana temporaria</em></td>
<td>LP <em>G. aculeatus</em></td>
<td>Caged L-fed</td>
<td>9.1 d</td>
<td>− 0.7 d</td>
<td>− 7%</td>
<td>Laurila et al. 2002</td>
</tr>
<tr>
<td><em>Rana temporaria</em></td>
<td>LP dragonfly <em>Aeschna</em> sp.</td>
<td>Caged L-fed</td>
<td>9.1 d</td>
<td>− 0.5 d</td>
<td>− 6%</td>
<td>Laurila et al. 2002</td>
</tr>
<tr>
<td><em>Rana temporaria</em></td>
<td>EP <em>Haemopis sanguineae</em></td>
<td>Caged E-fed</td>
<td>9.1 d</td>
<td>− 0.8 d</td>
<td>− 9%</td>
<td>Laurila et al. 2002</td>
</tr>
<tr>
<td><em>Rana temporaria</em></td>
<td>LP <em>G. aculeatus</em></td>
<td>Caged L-fed</td>
<td>6.8 d</td>
<td>+ 0.7 d</td>
<td>+ 10%</td>
<td>Laurila et al. 2002</td>
</tr>
<tr>
<td><em>Rana temporaria</em></td>
<td>LP dragonfly <em>Aeschna</em> sp.</td>
<td>Caged L-fed</td>
<td>6.8 d</td>
<td>none</td>
<td>0%</td>
<td>Laurila et al. 2002</td>
</tr>
<tr>
<td><em>Rana temporaria</em></td>
<td>EP <em>Haemopis sanguineae</em></td>
<td>Caged E-fed</td>
<td>6.8 d</td>
<td>none</td>
<td>0%</td>
<td>Laurila et al. 2002</td>
</tr>
<tr>
<td><em>Rana temporaria</em></td>
<td>EP pred. chem.</td>
<td>E-fed</td>
<td>217 h</td>
<td>− 11 h</td>
<td>− 5%</td>
<td>Capellán &amp; Nicieza 2007</td>
</tr>
<tr>
<td><em>Rana temporaria</em></td>
<td>E-fed pred. chem.</td>
<td>Caged E-fed</td>
<td>~ 351 h</td>
<td>− 29 h</td>
<td>− 8%</td>
<td>Capellán &amp; Nicieza 2010</td>
</tr>
<tr>
<td><em>Rana temporaria</em></td>
<td>Caged L-fed. pred. chem.</td>
<td>L-fed</td>
<td>~ 351 h</td>
<td>− 26 h</td>
<td>− 7%</td>
<td>Capellán &amp; Nicieza 2010</td>
</tr>
<tr>
<td><em>Rana temporaria</em></td>
<td>Unfed pred. chem.</td>
<td>Crashed E chem.</td>
<td>~ 351 h</td>
<td>none</td>
<td>0%</td>
<td>Capellán &amp; Nicieza 2010</td>
</tr>
<tr>
<td><em>Rana temporaria</em></td>
<td>Simulated egg predation</td>
<td>Crushed E chem.</td>
<td>351 h</td>
<td>− 6 h</td>
<td>− 2%</td>
<td>Capellán &amp; Nicieza 2010</td>
</tr>
</tbody>
</table>

$^a$ Responses of aquatic eggs to egg and larval predators and simulated predation cues

References for Table S1


