



# How do embryos assess risk? Vibrational cues in predator-induced hatching of red-eyed treefrogs

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I examined the role of vibrations in predator-induced early hatching of red-eyed treefrogs, *Agalychnis callidryas*. The arboreal eggs of *A. callidryas* hatch up to 30% early if attacked by egg-eating snakes. This induced hatching is a behavioural response that occurs once snakes begin physically disturbing the clutch, and is sufficiently rapid to allow most embryos to escape. Other intense but benign disturbances, such as tropical storms, do not induce such hatching. I used a miniature accelerometer to record vibrations in egg clutches during snake attacks and rainstorms, and analysed the recordings to identify parameters that distinguished disturbance types. Snake-induced vibrations were on average longer, more widely spaced, and of lower frequency than rain-induced vibrations. I performed three sets of vibration playbacks to examine the hatching response of embryos to different vibration patterns. (1) Playbacks of recorded snake attacks elicited more hatching than did rain recordings. (2) I edited snake and rain recordings by moving periods of stillness to clump together rain vibrations and extend intervals, and divide snake vibrations into shorter, more tightly spaced bits. In playbacks, clumped rain elicited more, and divided snake vibrations less hatching than did the original recordings. (3) Bursts of white noise with a constant vibration-to-interval ratio but different cycle durations elicited different levels of hatching. Vibrations alone were sufficient to induce early hatching, without chemical or visual cues from predators. Embryos also clearly distinguished among different vibration patterns and used cues in the gross temporal pattern in making their hatching decision.

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Antipredator defences can be critical, but are often costly (Sih 1987; Lima & Dill 1989). For inducible defences, including much antipredator behaviour, deployment of the defence only under conditions of risk reduces this cost (Kurban & Baldwin 1997; Tollrian & Harvell 1999). However, to effectively use inducible defences, organisms require information about the level of risk. Here I examine the use of vibrational cues in the predator-induced defensive early hatching of red-eyed treefrog, *Agalychnis callidryas*, embryos.

Substrate-borne vibration has received less attention than airborne and waterborne sound as information channels for animals; however, it is probably far more broadly used and important than this distribution of effort

suggests (Hill 2001a, b). Among conspecifics, vibration is used in courtship (Barth et al. 1988; Satou et al. 1991; Schmitt et al. 1994; Hill & Shadley 1997, 2001), parent-offspring communication (Cocroft 1999a, b), and other social interactions (Kirchner et al. 1994; Randall & Lewis 1997; Lewis et al. 2001; Mason & Narins 2001) in taxa from insects to mammals, and even humans (Levanen et al. 1998; Levanen & Hamdorf 2001). It is used by foragers to detect prey and other resources (Bleckmann 1985; Hanrahan & Kirchner 1994; Pfannenstiel et al. 1995; Meyhofer et al. 1997; Brownell & Van Hemmen 2001), and by prey to detect and respond to predators (Bacher et al. 1997; Randall & Matocq 1997).

From a prey perspective, vibration can indicate imminent danger of predation before physical contact occurs, and offers certain advantages over other information channels. Rather than indicating general, ongoing levels of risk or predator presence in the environment as chemical cues often do, vibration indicates the current

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activity of an individual predator. Moreover, as a by-product of movement, vibration may be more difficult for a predator to avoid producing than sound (although it may be concealed among background vibrations; Wilcox et al. 1996). The detection of vibration is not limited by the physical orientation of the prey, as with vision, thus it may require less investment in vigilance. Furthermore, it is unlikely to be obscured by visual barriers between predator and prey. From a predator perspective, vibrations have similar advantages, and may allow the detection of prey that are not evident in other sensory modalities (e.g. buried prey; Brownell & Van Hemmen 2001). However, the vibrations produced by foraging predators, and by most prey activities, are not stereotyped communication signals that have evolved to be clearly distinct from background vibrations. They are likely to be much more variable than communication signals, and potentially to overlap more with vibrations from other sources. Thus, foraging predators and vulnerable prey face a problem in distinguishing salient from irrelevant vibrations.

Embryos are often highly vulnerable, suffering high mortality from predation and pathogen infection (Orians & Janzen 1974; Howard 1978; Green 1999). None the less, in the last decade it has become increasingly clear that they are not completely defenceless, nor solely reliant on parentally provided defence. In several species of amphibians, embryos alter their hatching stage in response to risk of predation or pathogen infection (Sih & Moore 1993; Warkentin 1995; Vonesh 2000; Chivers et al. 2001; Warkentin et al. 2001; Laurila 2002; Johnson et al. 2003). Pathogen-induced early hatching has also been demonstrated in fish (Wedekind 2002). Thus, these embryos appear to be sensitive to cues provided by their predators and pathogens.

The best-studied case of predator-induced early hatching is the red-eyed treefrog. These frogs inhabit lowland wet forests from the Yucatan to Panama, where they typically breed in seasonal ponds and swamps. The eggs are deposited on vegetation overhanging the water, and tadpoles fall into the water upon hatching. Vulnerability to aquatic predators declines with development, and undisturbed eggs hatch relatively late (6–7 days old in Panama, 7–8 days old in Costa Rica), avoiding the highest risk period in the water. However, embryos hatch up to 30% earlier if attacked by egg-eating snakes or wasps, or infected by pathogenic fungus (Warkentin 1995, 2000; Warkentin et al. 2001).

The response to predators is not a general response to local predator density, but rather a specific response to attacks on individual clutches. Shortly after a predator begins biting an egg clutch, the embryos begin vigorous movements that rupture their egg capsules and propel them from the clutch within seconds, making their escape (Warkentin 1995, 2000). Thus, the escape behaviour appears to be a response to the physical disturbance of clutches. However, egg predators are not the only source of physical disturbance to clutches. For instance, clutches are frequently subjected to tropical storms, which last far longer than predator attacks and can be forceful enough to knock eggs off of clutches, yet do not induce premature hatching (Warkentin 1995, personal observation).

Here I examine the vibrational information available to embryos in an important dangerous disturbance, snake attack, and the most common benign disturbance, rain. I then ask whether the predator-induced vibrations alone, without any chemical or visual cues from predators, can stimulate early hatching, whether embryos can distinguish between the vibrations of snake attacks and rainstorms, and whether simple elements of the temporal pattern contribute to this distinction.

## VIBRATION RECORDINGS

### Methods

#### *Animal collection and care*

I collected young *A. callidryas* egg clutches on leaves from Ocelot Pond, 2 km south of Gamboa, Panama. Clutches were brought to an open-air laboratory in Gamboa where any dead (possibly unfertilized) or developmentally abnormal eggs were removed. Each clutch was mounted on a 5 × 10-cm plastic card for support, excess leaf area was trimmed if necessary, and the clutch was set over water in a plastic cup. Cups were placed in screen-covered containers to exclude insects, and eggs were misted with rainwater several times daily to prevent desiccation. All hatchlings were returned to Ocelot Pond after experiments. I collected two parrot snakes, *Leptophis ahaetulla*, and three cat-eyed snakes, *Leptodeira annulata*, by hand from Ocelot Pond and the Gamboa area, and maintained them in screen cages (*Leptophis*) or aquaria (*Leptodeira*) with vegetation to climb on and hide in, and with a tray of water that also served to catch hatching tadpoles. Snakes were offered *A. callidryas* egg clutches every few days until they were readily feeding in captivity. Snakes were released at their collection sites after egg-eating vibrations were recorded. This research was conducted during May–August 2000 and 2001 under permits from the Panamanian Autoridad Nacional del Ambiente. The research protocol, including animal use, was approved by the Smithsonian Tropical Research Institute in April 2000.

#### *Vibration recordings*

I used a miniature isotron accelerometer (0.2 g, Model 25B, Endevco, San Juan Capistrano, California, U.S.A.) as a transducer to record vibrations in egg clutches. The accelerometer was first potted in a thin layer of silicone sealant, to keep it dry, then inserted into the clutch among the eggs, adding about 5% to the mass of an average clutch. The accelerometer wire was taped to the clutch support card about 3 cm away from the accelerometer. Thus, the accelerometer was free to move with the eggs as the clutch was deformed by external forces or, on a smaller scale, by the motion of embryos. The movement of the accelerometer was not perfectly coupled with any individual egg but, like eggs, it was moved by the motion of the surrounding eggs and jelly. The accelerometer was powered by a signal conditioner (Model 4416B, Endevco) and the output recorded using Canary bioacoustic software (V1.2.4, Cornell Laboratory of Ornithology, Ithaca, New York, U.S.A.) at 22.1 kHz on a Macintosh G3 laptop

computer. All components were battery powered to reduce electrical noise.

For recordings, I taped the card supporting the clutch and its embedded accelerometer to a jar of water (~1 kg) as a solid support structure. This method of mounting duplicates the common vertical position of clutches, while standardizing position and support structure. It minimizes rigid body motions of the entire clutch, mimicking the natural context of clutches laid on tree trunks, and simplifies the detection of the forces applied directly to the egg clutch, which are likely to carry the information that is most relevant to the embryos. Accelerometers were implanted into 3-day-old clutches, which are not capable of hatching, and recordings were made when clutches were 4 days old, when embryos are just becoming capable of hatching, or at 5 days, when all embryos are capable of hatching, but rarely hatch if undisturbed.

To record snake attacks, I placed a clutch with an embedded accelerometer into a cage or aquarium with a snake. I recorded the accelerometer output and simultaneously videotaped the clutch using a digital video camera with infrared illumination (Sony DCR-TRV120). Due to recording time (file size) limits, I reset the vibration recording every 15 min as necessary, until the snake attacked the clutch. Likewise, the video recording was reset every hour, as long as necessary. The videorecord was used to identify attacks and the source of each vibrational event within attacks (e.g. snake tongue flick, snake bite, embryo hatching). I also used it to identify, and exclude from analysis, episodes when the snakes attempted to swallow the accelerometer. I only analysed attacks where sufficient snake-clutch interaction occurred to induce embryos to begin hatching before the snake started trying to swallow the accelerometer. By this criterion, I recorded 12 useable snake attacks, seven by *Leptodeira* and five by *Leptophis*, including two to three attacks per individual snake, and an additional four unuseable attacks (16 clutches used in total).

To record rain, at the beginning of a storm or in anticipation of an impending storm, I placed a clutch with an embedded accelerometer outside in a clear area where rain fell directly on it. The accelerometer output was recorded as above, but clutches were not videotaped. I recorded seven rainstorms, with rainfall ranging from 3.6 to 12.6 mm in 45 min, using seven egg clutches.

#### *Analysis of vibration recordings*

I examined four simple characteristics of the recorded vibrations: duration, peak acceleration and dominant frequency of vibration events, and the interval between events. All vibration analyses were conducted using Canary 1.2.4. For snake attacks, I analysed the entire period (38–480 s) from the snake's first contact with a clutch until either all the eggs had hatched ( $N = 2$ ), or the snake started eating the accelerometer ( $N = 8$ ), or biting and hatching had ceased even though some eggs remained on the clutch ( $N = 2$ ). Recordings were first high-pass filtered at 2 Hz to remove DC offset, then all events with an amplitude of at least  $2 \text{ m/s}^2$  were analysed. The background noise floor was  $1.2 \text{ m/s}^2$ . For rainstorms,

I analysed the 30 s of the recording with the highest root-mean-square amplitude. To measure dominant frequency of each event I used fast Fourier transforms, with a filter bandwidth of 5.38 Hz and a frame length of 8192 points. Because the amplitude of events within snake attacks, and within storms, varied greatly, I also calculated frequency spectra of entire snake attacks, and extended periods of rain from each storm (375–899 s, mean = 724 s) to assess the overall distribution of energy across frequencies. I measured dominant frequency, and the lowest and highest frequencies with 10% of the power/Hz of the dominant frequency. I also measured the amplitude of the five hardest raindrops in each storm.

The duration of 'events' within disturbance sequences and the length of intervals between them depend critically on how those events are defined. For snake attacks, because it is not yet clear what embryos attend to, I measured the following types of 'events'. (1) Entire periods of continuous snake mouth contact with the clutch, including all vibrations induced by the contact, any still intervals within the contact period, and the vibrations associated with breaking contact. (2) Periods of continuous vibration during (1) above (some snake contact periods included several periods of vibration, separated by periods where vibration dropped to the background level; others consisted of one continuous vibration period). (3) Embryo vibrations when the snake was not in contact with the clutch. Vibrations concurrent with hatching on the videorecord were considered hatching vibrations. All other vibrations, associated neither with visible hatching nor with snake contact, were considered to be other embryo vibrations. In some cases, concurrent embryo movements within the egg were visible in the videorecord. Vibrations caused by embryo movements that occurred during periods of snake contact could not be separated from the snake-induced vibrations, and are thus included in (1) and (2) above.

Because it is not yet clear whether attacked embryos attend to vibrations from their siblings, I also pooled (2) and (3) to describe the complete series of vibrations that occurred in snake attacks, regardless of the source of the movement. For rainstorms, I could not separate vibrations induced by raindrops from those induced by embryos. Also, all events in rainstorms were vibrationally defined (i.e. when raindrops fell in close succession so that the impact of one drop extended the vibrations induced by a previous drop, I measured it as a single longer event, rather than two short overlapping events).

#### *Statistical comparison of vibration patterns*

To test whether characteristics of the vibration patterns differ between vibrations caused by rain and snakes, I used a single value for each storm (i.e. I averaged across vibration events for measures of individual events;  $N_{\text{storms}} = 7$ ). Each storm was recorded using a different egg clutch. For snakes, to avoid pseudoreplication (Hurlbert 1984; Wiley 2003), I first calculated the values for each attack, then averaged these across the two or three attacks by each individual. Due to the low total number of snakes, I pooled the two species to compare snakes versus rain

( $N_{\text{snakes}} = 5$ ). I used medians tests (Sokal & Rohlf 1995) due to non-normality and heteroscedasticity of the data.

To describe the full range in the patterns of vibration, I considered all attacks individually, and separated attacks by species of snake. For an embryo needing to distinguish among vibrations from different sources, the range of overlap may be at least as important as a difference in means.

## Results

Although there was substantial variation within and among snake attacks and storms, the overall vibration patterns were distinctive (Figs 1–4, Tables 1–3).

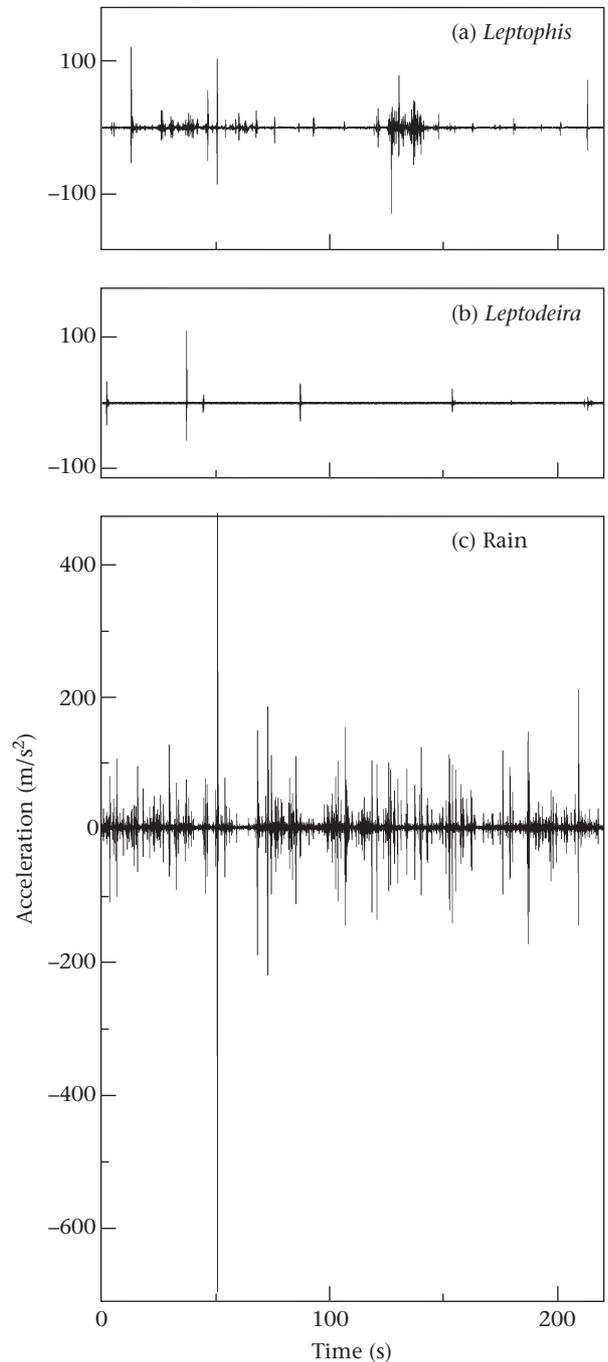
### Amplitude of acceleration

Root-mean-square acceleration, mean peak acceleration and maximum overall acceleration were statistically indistinguishable between snake attacks and rainstorms (Tables 1, 2). Acceleration amplitudes varied substantially within both disturbance types, and this variation was similar across disturbance types (Table 1, Figs 1, 3). However, the strongest vibrations were recorded from rain. Embryos produced only low-amplitude vibrations, not the full acceleration range produced by snakes and rain (Fig. 3).

### Duration and interval

The *Leptophis* fed by walking their jaws over large clumps of eggs, sometimes pulling back and then biting forward again before tearing off the mouthful. Thus, the entire snake–clutch contact periods were long (Table 2, Figs 1, 2). In some cases, these contact periods were broken into multiple vibrational events, but on average these were still relatively long (Table 2, Fig. 3). *Leptodeira* mostly fed by taking one or two eggs at a time in a series of short strikes (Figs 1, 2), thus the snake–clutch contact periods were shorter than for *Leptophis*. Some *Leptodeira* bites also had a vibrational substructure, but there was less difference between behaviourally defined contact periods and vibrationally defined movements than in *Leptophis* (Table 2). Vibrations caused by embryos were shorter than those caused by snakes; thus, complete attack sequences, which included embryos vibrations, had a wide range of event durations (Table 2). Event durations in storms were significantly shorter than snake-induced vibrations (Tables 1, 2, Figs 1, 2). Of the 532 events measured from the hardest 30 s of each storm, 64% lasted less than 0.1 s, and only 3.6% lasted longer than 1 s, although the single longest event was 11.9 s. The duration of rain-induced vibrations was relatively more variable than that of snake vibrations (Table 1). Although many rain vibrations were clearly caused by single drops, in hard rain a rapid series of drops caused extended periods of vibration in the egg clutches.

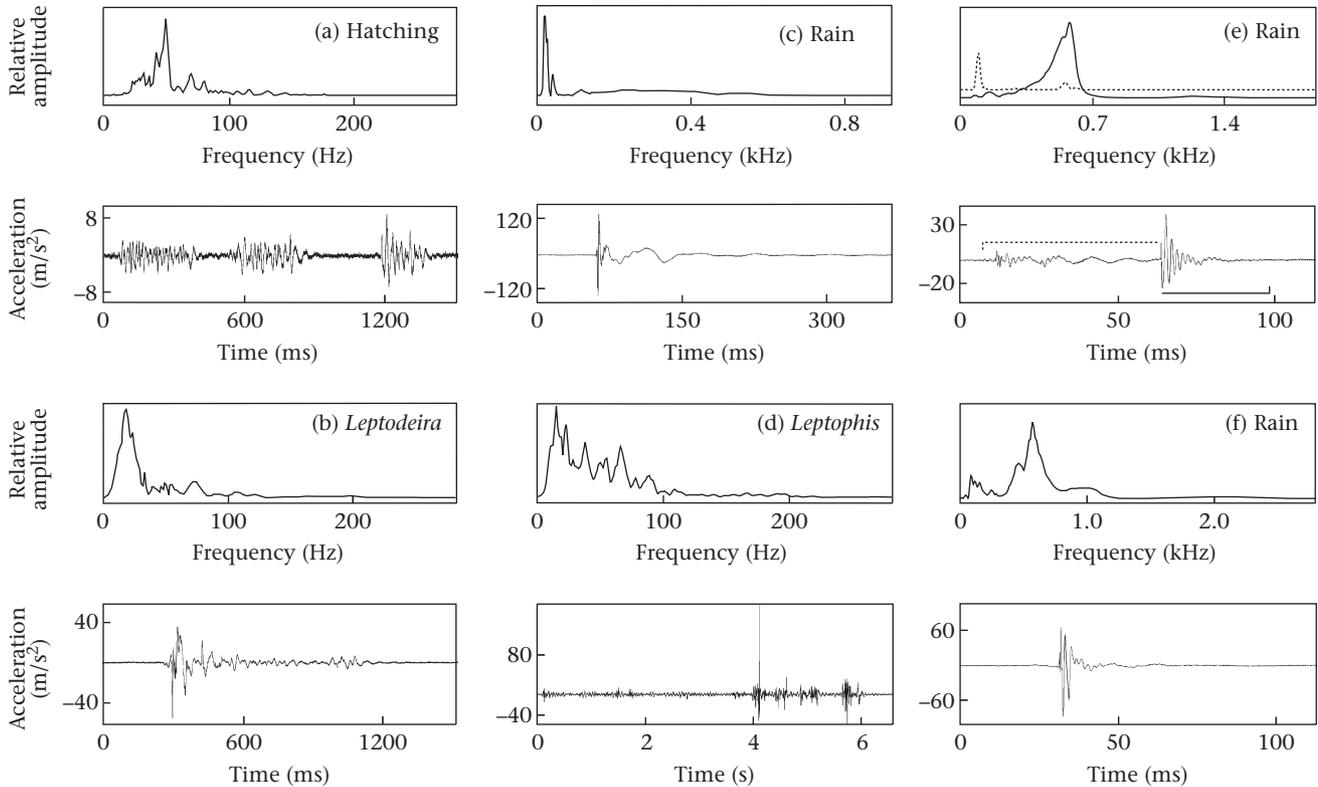
Like durations, intervals between vibration events in storms were also short, on average 0.2 s and ranging up to only 3.1 s during periods of hard rain. Some intervals between snake movements within contact periods were short, making the intervals in snake attacks more variable than in storms (Table 1). However, the average intervals between snake vibrations were far longer than the intervals between rain-induced vibrations (Tables 1, 2, Fig. 3).



**Figure 1.** Examples of vibrations recorded from *A. callidryas* egg clutches in snake attacks and rainstorms. (a) A single, complete, *Leptophis* attack in which all embryos were eaten or hatched. The snake performed two extended biting/pulling sequences, shown from 9–64 s and 122–160 s in the waveform graph. Other vibrations were caused by embryos. This recording was used as a playback stimulus. (b) A segment of a *Leptodeira* attack showing shorter, widely spaced bites. (c) A period of hard rain, showing tightly spaced, short vibrations.

### Frequency

Considering attacks as a whole, or long sections of storms, the dominant frequency of vibrations induced in egg clutches was usually low, and not significantly



**Figure 2.** Examples of vibrations recorded from *A. callidryas* clutches in snake attacks and rainstorms. For each vibration, the frequency spectrum is plotted above, showing relative amplitude of each frequency on a linear scale. Note that the range of frequencies, and hence the X-axis scale, differs among vibrations. The waveform, showing amplitude of acceleration over time is plotted below. Note that both peak amplitudes and durations differ substantially among vibrations, thus axes are to different scales. (a) Three vibrations from embryos hatching. (b) A single *Leptodeira* bite. (d) A single *Leptophis* biting period, in which the snake was in continuous contact with the clutch. (c, e and f) Raindrop-induced vibrations, showing some of the variation among them. (c) A single, moderately high-amplitude, low-frequency vibration. (e) Two raindrops in quick succession, the first inducing a low-frequency vibration (dotted line in spectrum, offset vertically for clarity), and the second inducing a higher-frequency vibration (solid line in spectrum). (f) A single raindrop vibration, with a fairly high dominant frequency, but a broader frequency spread.

different across disturbance types, falling between 12 and 40 Hz in all attacks and all but two storms (Tables 1, 3). The range of frequencies with at least 10% of the peak power/Hz tended to be broader in storms, but was not significantly so (Tables 1, 3).

The frequencies of snake- and rain-induced vibrations were more distinct when considered as series of individual vibration events (Tables 1, 2, Fig. 4). During attacks, almost all snake-induced vibrations and over three-quarters of embryo vibrations had dominant frequencies under 60 Hz, whereas three-quarters of rain-induced vibrations had dominant frequencies over 60 Hz, including a substantial proportion of events with dominant frequencies of several hundred hertz. Thus, the dominant frequencies of rain-induced vibrations were on average higher, and significantly more variable than those of snake vibrations (Table 1).

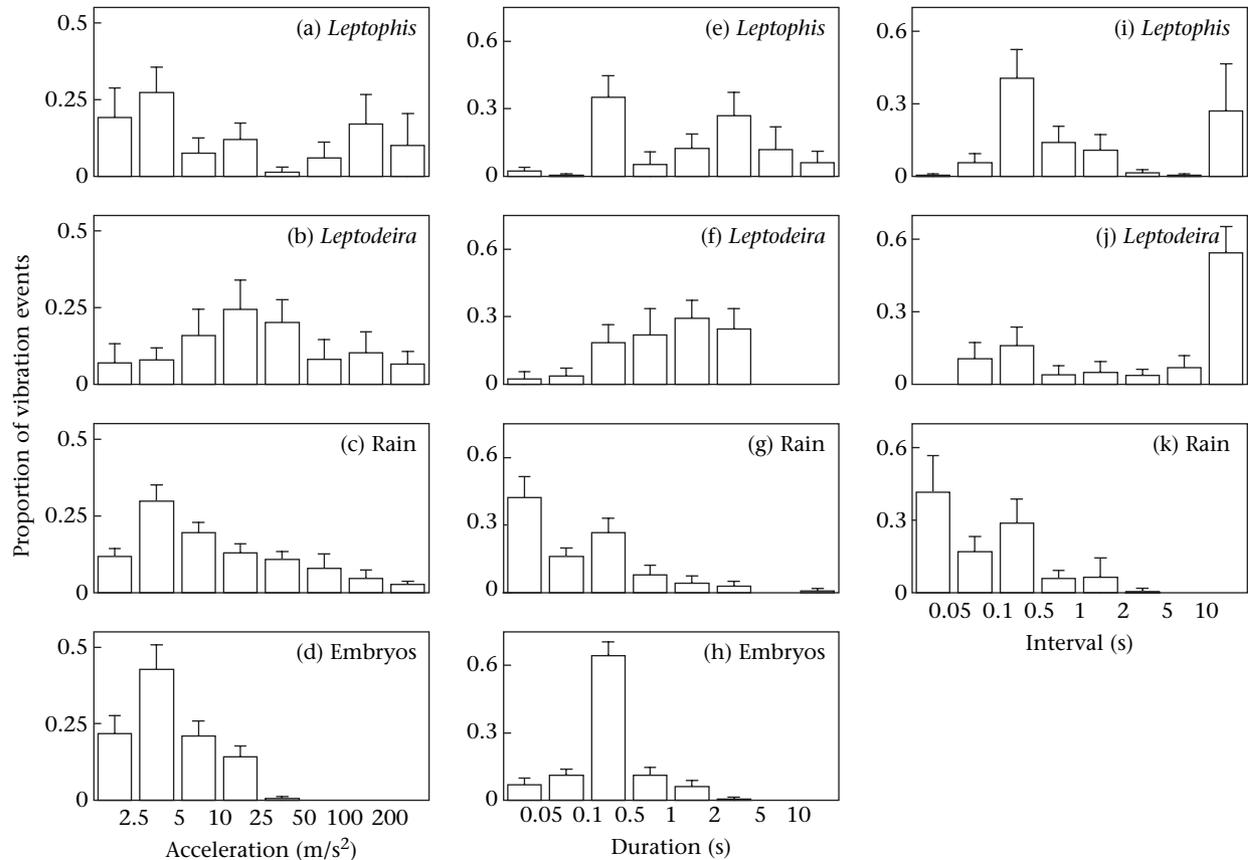
## VIBRATION PLAYBACK EXPERIMENTS

### Methods

To assess embryo responses to vibrational patterns, I experimentally exposed egg clutches to artificial vibrations

and monitored their hatching. The vibration playback system consisted of an electrodynamic minishaker (Model 4810, Brüel & Kjaer) controlled by Canary 1.2.4 on a Macintosh G3 laptop computer, via an Optimus MPA-50 amplifier (Radio Shack). The minishaker-clutch interface (MCI) was a set of eight blunt tines, constructed of 18-gauge galvanized wire in tight loops spaced 8 mm apart vertically, in two rows of four spaced 10 mm apart, at the end of a rigid wire stinger (20 cm from MCI tip to shaker attachment point). Egg diameters are typically 3–5 mm. The minishaker with attached MCI was hung from a wooden stand above a tray of aged tap water. Thus, the eggs were moved up and down, and hatchlings fell into the water. I attached playback clutches, on their plastic cards, to a flat-sided plastic stand (ca. 1.5 kg) with the long axis of the clutch oriented vertically. I then carefully moved the clutch and stand forward so that the MCI tines entered the clutch between eggs.

Only healthy clutches that I could set up to contact at least five MCI tines were used for playbacks. After insertion of the MCI, and any hatching induced by that procedure, I allowed five hatching-free minutes for acclimation before the start of a playback. If 25% or more of a clutch hatched during set-up, I did not use that clutch in



**Figure 3.** Distribution of peak acceleration (a–d) and duration (e–h) of vibration events, and intervals (i–k) between events caused by *Leptophis ahaetulla*, *Leptodeira annulata*, rain and embryos. Data are mean  $\pm$  SE proportions of events in each range of values, calculated across clutches ( $N_{Leptophis} = 5$ ,  $N_{Leptodeira} = 7$ ,  $N_{rain} = 7$ ,  $N_{embryos} = 11$ ). The snake interval distributions include both brief still intervals while the snake's mouth was on the clutch, and longer intervals while the snake was not in contact with the clutch. Snake durations are for vibrationally defined events within contact periods. Embryo vibrations were measured only when the snake was not in contact with the clutch.

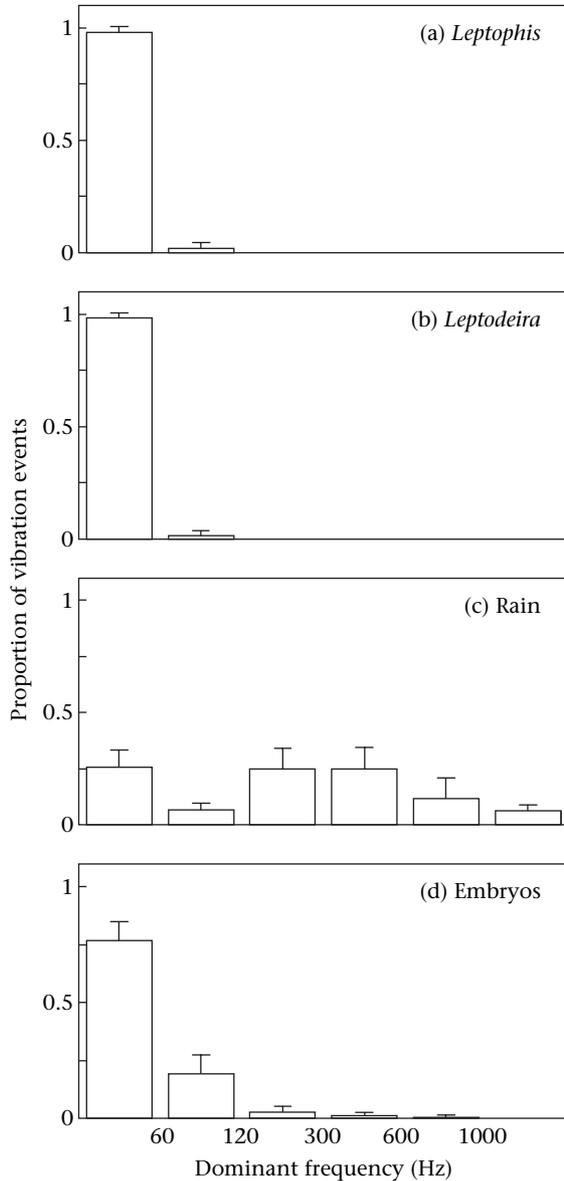
a playback. Hatched embryos were counted every minute for 10 min from the start of the playback. Each clutch was only used once, and the MCI was rinsed with rainwater between trials to remove any perivitelline fluid from hatched eggs. To limit variation in the hatching response due to egg development and diel cycle, all playbacks were conducted during 0730–1300 hours, using 5-day-old clutches. Development is highly synchronous within clutches and among clutches laid at the same time and developing together at a site (Warkentin 1995, 1999b). Sets of stimuli to be compared were presented in random order within temporal blocks.

#### Playback stimuli

My initial playbacks addressed two questions. (1) Can embryos hatch in response to vibrational cues in a snake attack, without any other cues (e.g. chemical or visual) indicating the source of disturbance? (2) Can embryos distinguish vibrations associated with a dangerous disturbance (snake attack) from those associated with a benign disturbance (rain), in the absence of any other cues? To address these questions I used two snake stimuli ( $N = 10$  clutches each) contrasted with four rain stimuli ( $N = 5$  clutches each). The first snake stimulus was the complete

240 s of a recorded *Leptophis* attack on a 5-day-old clutch in which 24% of the embryos were eaten, the rest hatched, and no accelerometer eating occurred (Fig. 1a). The second snake stimulus was a composite of the initial parts of three *Leptophis* attacks, before accelerometer eating occurred, spliced together to give a total of 205 s (42 + 63 + 100 s; see Fig. 5a). Each snake stimulus was paired with two rain sequences matched to it for duration and root-mean-square (RMS) acceleration. Matching by RMS acceleration conservatively makes the peak accelerations in the rain stimuli higher than those in the snake stimuli. Playback levels were initially set by visual observation of clutches and confirmed to be within the amplitude range of natural snake attacks and storms by re-recording vibrations from playback clutches.

A clear difference between snake attacks and rainstorms is the gross temporal pattern of disturbance: snake bites last longer and are spaced at longer intervals than raindrops. Thus, I asked whether embryos attend to this kind of information. I constructed four pairs of stimuli that differed only in gross temporal pattern by editing the two snake stimuli, above, and two 300-s sequences of hard rain from different storms (Fig. 5). First, I removed background electrical noise between vibration events. Then, to create 'rainified' snake stimuli, I shortened vibration events and



**Figure 4.** Distribution of dominant frequencies of vibration events in *A. callidryas* egg clutches caused by (a) *Leptophis*, (b) *Leptodeira*, (c) rain and (d) embryos. Data are mean  $\pm$  SE proportions of events in each frequency range, calculated across clutches ( $N_{Leptophis} = 5$ ,  $N_{Leptodeira} = 7$ ,  $N_{rain} = 7$ ,  $N_{embryos} = 11$ ). Data in (a) and (b) are from vibrationally defined events within snake-clutch contact periods.

intervals, making the temporal pattern more like rain. For the first snake stimulus, I used only the original 240 s, moving parts of still intervals into the disturbances to divide them up. Edits were haphazard to generate a variety of disturbance and interval lengths; the longest disturbance was 350 ms, and the longest interval was 800 ms. For the composite snake stimulus, I added additional vibration-free time between the three attack sequences to extend the total time to 450 s, and used this additional time, as well as still intervals within the original attacks, to break up the disturbances. All disturbances were less than 250 ms. The longest interval was 1.5 s, and most were under 500 ms. To construct ‘snakeified’ rain stimuli, I clumped together series of disturbances and intervals, to

**Table 1.** Statistical comparison of vibrations in egg clutches of *Agalychnis callidryas* caused by rainstorms versus snake attacks (*Leptophis* and *Leptodeira* combined)

Variable	$p^*$
A. Characteristics of individual vibration events within attacks or storms	
Mean peak acceleration	1
CV of peak acceleration	0.24
Mean duration	0.015
CV of duration	0.015
Mean interval between vibrations	0.015
CV of interval	0.029
Mean dominant frequency	0.015
CV of dominant frequency	0.015
B. Characteristics of entire attacks, or long periods within storms	
Peak acceleration	0.24
Root-mean-square acceleration	1
Dominant frequency	1
Frequency range with > 10% of peak power	0.24

Means and coefficients of variation (CV) compared are for each individual storm ( $N = 7$ ) or snake ( $N = 5$ ). Snake vibrations in (A) are vibrationally defined events within periods when the snake’s mouth was in contact with the clutch, or the clutch was still vibrating just after being released by the snake.

\*Medians test for equality, two-tailed Fisher’s exact test.

lengthen them and make the temporal pattern more like snake attacks. For the first edited rain stimulus, I clumped together all the raindrops in each 25-s period, creating 12 disturbance events of 4.2–6.8 s each. For the second edited rain stimulus, I clumped drops in 60-s periods, yielding five disturbance events of 12.9–21.2 s each. Edits were made at zero crossings to avoid introducing clicks, nothing was added or removed, and the order of vibration events was unaltered. I examined the frequency spectra of original and edited stimuli to confirm that my edits had not changed the distribution of energy. The original vibration patterns and their edited partners were presented to 10 clutches each.

As a second way to assess whether embryos attend to the temporal pattern of disturbance, I constructed four purely synthetic stimuli, composed of 0–11 kHz white noise in a 1:4 ratio of vibration to stillness in different cycle durations as follows: 0.12/0.6 s, 1.2/6 s, 12/60 s and 120/600 s. These playbacks were matched for RMS and peak amplitude. All stimuli began with a period of vibration and were played for 10 min, to 10 clutches each. These stimuli do not match the average snake and rain temporal patterns, since that is not possible using a single duration: interval ratio while keeping total energy and amplitude constant. However, the 1:4 ratio lies between snake and rain patterns; the shortest cycle is the most rain-like, the middle two are both somewhat snake-like, and the longest is neither snake-like nor rain-like.

## Results

Both the single and the composite *Leptophis* recordings elicited more hatching on playback than did the

**Table 2.** Characteristics of vibration events recorded in 4–5-day-old *Agalychnis callidryas* egg clutches during snake attacks and rainstorms

Source of vibration*	Acceleration (peak, m/s <sup>2</sup> )	Duration (s)	Interval (s)	Dominant frequency (Hz)
Snakes: entire periods of continuous contact				
<i>Leptophis</i>	117±30 64, 1.8 (17–283)	23.1±8.7 6.8, 1.4 (3.7–55.3)	38.4±13.1 1 (1.9–66.1)	21±3.0 4, 1.8 (16–35)
<i>Leptodeira</i>	73±23 72, 7.1 (5–730)	2.0±0.24 1.2, 7.1 (0.4–7.9)	42.8±6.8 35, 5.9 (0.1–210)	25±4.1 5, 7.1 (13–62)
Snakes: individual, vibrationally defined movements				
<i>Leptophis</i>	86±40 61, 17 (2–283)	6.3±3.4 1.3, 16.6 (0.02–19.4)	24.1±13.8 4.0, 20.2 (0.04–103)	24±3.8 8, 17 (9–114)
<i>Leptodeira</i>	54±19 67, 9.6 (2–730)	1.3±0.24 0.8, 9.6 (0.05–4.5)	30.9±7.25 35.8, 8.6 (0.06–210)	26±4.2 7, 9.6 (13–65)
Snake attack sequences, including snake and embryo movements				
<i>Leptophis</i>	20±6 40, 29.6 (2–283)	1.1±0.2 2.0, 29.2 (0.005–19.4)	2.7±1.1 3.6, 28.8 (0.005–30.3)	41±8.1 46, 29.6 (9–554)
<i>Leptodeira</i>	28±11 51, 26 (2–730)	0.8±0.15 0.8, 26 (0.03–4.5)	11.3±2.27 15.2, 25 (0.1–100)	50±7.4 45, 26 (13–657)
Embryo movements				
Hatching	7±0.7 5, 6 (2–24)	0.5±0.06 0.3, 6 (0.1–3.0)		44±6.4 10, 6 (16–109)
Other	5±0.8 3, 10 (2–30)	0.2±0.04 0.2, 10 (0.005–1.5)		60±8.5 63, 10 (14–657)
Rainstorms				
30-s sequences	31±7 71, 76 (2–979)	0.4±0.2 0.6, 76 (0.005–11.9)†	0.2±0.1 0.2, 75 (0.001–3.1)	368±55 416, 76 (5–6821)
Hardest drops	387±50 150, 5 (130–979)			

\*For each vibration source, the data are organized as follows: line 1: means of within-recording means ± SE of the mean across recordings; line 2: means of within-recording SD, mean  $N$  of events recorded from each clutch; line 3: full range of values across all clutches. Sample sizes of events within recordings vary because not all parameters were measurable from all events (e.g. natural bite duration was sometimes altered by attempts to swallow the accelerometer). Hatching occurred in all snake attacks, but hatching vibrations were not always separable from snake vibrations. Number of recordings (or clutches) for each disturbance type: *Leptophis* = 5, *Leptodeira* = 7, rain = 7, hatching = 9, other embryo = 11.

†Some periods of continuous vibration in rainstorms include impacts from multiple raindrops that fell in quick succession.

duration- and amplitude-matched rain sequences with which they were paired (Fig. 6; single attack: Mann–Whitney  $U$  test:  $U = 0$ , test  $N_1 = N_2 = 10$ ,  $P = 0.0001$ ; composite:  $U = 1$ ,  $N_1 = N_2 = 10$ ,  $P = 0.0002$ ). Hatching began in the first minute of playback, and most hatching occurred in the first 4 min, although a few embryos hatched after the playback had ended. Hatching levels did not differ significantly between the two snake stimuli, or among the four rain stimuli (snakes:  $U = 45$ ,  $N_1 = N_2 = 10$ ,  $P = 0.7$ ; rain: Kruskal–Wallis test:  $\chi^2_3 = 5.38$ ,  $P = 0.15$ ).

In the playbacks of edited stimuli in all cases, the more snake-like pattern elicited more hatching than the more rain-like pattern. Both clumped rain vibrations elicited

more hatching than the original rain sequences from which they were made (Mann–Whitney  $U$  test: set 1:  $U = 22$ ,  $P = 0.03$ ; set 2:  $U = 6$ ,  $P = 0.0009$ ; Fig. 7a, b). Both divided snake vibrations elicited less hatching than the original snake sequences from which they were created (single attack:  $U = 89$ ,  $P = 0.003$ ; composite:  $U = 9$ ,  $P = 0.002$ ; Fig. 7c, d).

In the playbacks of synthetic white noise, different cycle durations elicited different levels of hatching (Kruskal–Wallis test:  $\chi^2_3 = 24.62$ ,  $P < 0.0001$ ; Fig. 8). The most hatching occurred in playbacks of the 1.2:4.8 s vibration-to-stillness ratio, with less hatching in both shorter and longer cycles.

**Table 3.** Distribution of energy across vibration frequencies in *Agalychnis callidryas* egg clutches during entire snake attacks and extended periods of rain

Disturbance	Period analysed (s)	Dominant frequency (Hz)	High and low frequencies with 10% of peak energy
<i>Leptophis</i>	136 ± 47 (41–205)	21 ± 4 (12–35)	7 ± 1.6 to 76 ± 9 (3–11) to (52–97)
<i>Leptodeira</i>	345 ± 80 (105–714)	23 ± 4 (15–30)	8 ± 0.4 to 82 ± 17 (7–10) to (40–166)
Rainstorms	725 ± 81 (375–889)	79 ± 41 (16–299)	15 ± 4 to 501 ± 130 (8–39) to (61–994)

Data are means ± SEs and ranges for N = 5 *Leptophis* attacks, 7 *Leptodeira* attacks and 7 rainstorms.

**DISCUSSION**

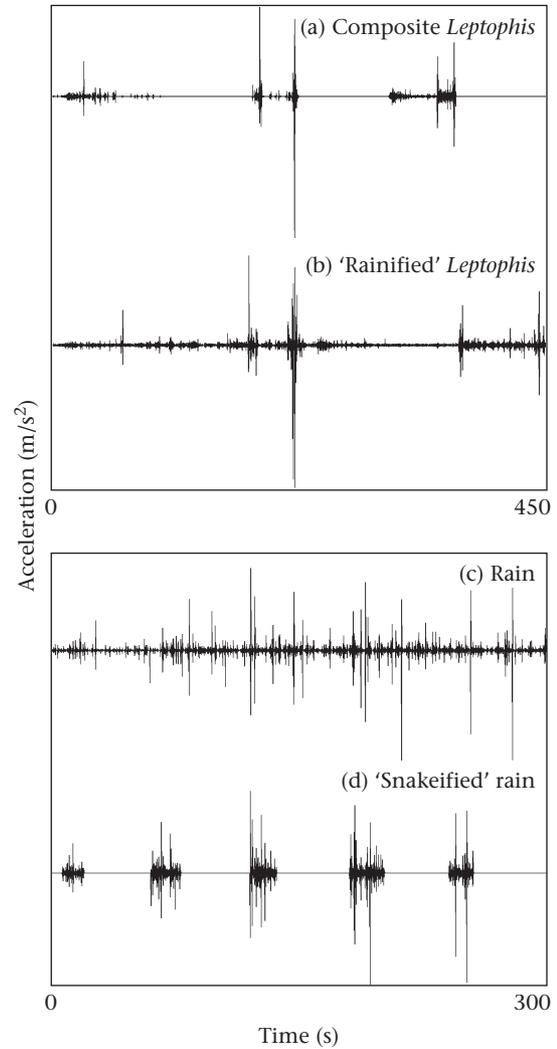
Substantial vibrations are elicited in the egg clutches of red-eyed treefrogs by common benign and dangerous natural disturbances, and the embryos use information carried by those vibrations to make the first critical behavioural decision of their lives: when to hatch. Rapid, early hatching in response to attack by egg predators allows embryos that would otherwise be eaten to survive (Warkentin 1995, 2000). However, the greater vulnerability of earlier hatchlings to tadpole predators imposes a cost to this defence (Warkentin 1995, 1999a). Thus, accurate assessment of the level of risk in the egg is critical.

Substrate-borne vibrations can be an immediate, local and reliable indicator of risk (e.g. Bacher et al. 1996, 1997; Meyhofer et al. 1997). All predator movements in contact with a substrate will induce some vibrations, and prey in contact with the same substrate may detect these vibrations without investing in specific, potentially costly, vigilance behaviours. However, there are also many benign sources of vibration in the environment. Thus, vibration per se is not a reliable indicator of risk, and prey would benefit from distinguishing among vibrations from different sources.

**Vibration Recordings**

For red-eyed treefrog embryos, snakes are an important predator, consuming over half the eggs at some sites (Warkentin 1995), and tropical storms are a frequent benign disturbance. My recordings of vibrations in egg clutches under these two disturbance types indicate that although both are variable, nonstereotyped patterns, they differ in several simple characteristics.

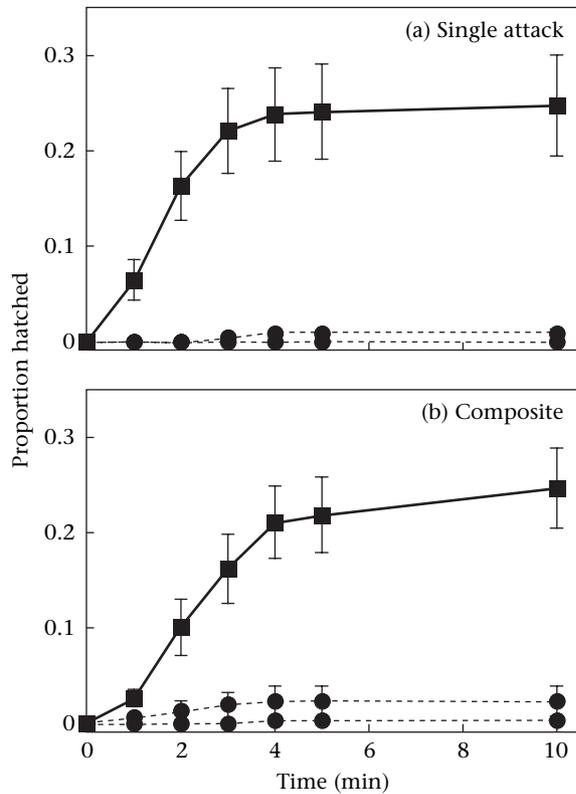
The absolute amount of disturbance, measured as root-mean-square acceleration over a period of time or as peak acceleration of individual vibrations, is broadly overlapping between snake attacks and rainstorms, and appears uninformative in distinguishing between them. Indeed, the highest accelerations I recorded were in rainstorms, so embryos clearly cannot presume that an intense disturbance is dangerous. Vibrations caused by embryos themselves are of relatively low intensity, although clearly



**Figure 5.** Examples of vibration patterns of (a) original and (b) divided, ‘rainified’ snake stimuli, and (c) original and (d) clumped, ‘snakeified’ rain stimuli, used in playback experiments. The original snake stimulus was composed of the start of three parrot snake attacks, spliced together. These same vibrations, with less intervening space, were used in the snake versus rain playbacks.

detectable. Thus, the only reliable information carried by intensity may be that vibrations above a certain amplitude indicate a source of disturbance external to the clutch.

Vibration duration and frequency, and the interval length between vibrations are all more informative than amplitude. Snakes cause longer, more widely spaced vibrations than do raindrops, and rain causes higher-frequency vibrations than do snakes. However, there is overlap between snake attacks and rain in these parameters. Snakes make some short, tightly spaced movements within contact periods. Raindrops sometimes run together to produce longer periods of continuous vibration, and a substantial proportion of raindrops produce low-frequency vibrations. Thus, many individual vibration events are likely to be unclassifiable based on these simple parameters. However, the overall patterns are clearly distinguishable. Combining parameters would improve the separation of disturbance types. For instance, rain



**Figure 6.** Hatching response of *A. callidryas* embryos to playbacks of the vibrations recorded in egg clutches during snake attacks and rainstorms. Solid lines and square symbols indicate responses to snake stimuli, dotted lines and round symbols indicate rain stimuli. Each snake stimulus was paired with two rain stimuli, matched for duration and root-mean-square acceleration. In (a), the stimulus was a single *Leptophis* attack (see Fig. 1a); in (b), it was a composite of parts of three attacks (see Fig. 5a). Data are means  $\pm$  SE for  $N = 10$  clutches/snake stimulus,  $N = 5$  clutches/rain stimulus.

events of long duration are unlikely to be separated by long intervals. Similarly, using series of events rather than single events would be more reliable. Rain does produce low-frequency vibrations, but a series of events without any higher-frequency vibrations is unlikely to be due to rain. Thus, these three simple parameters, assessed in combination over a short series of vibrations, appear sufficient to distinguish snake attacks from rainstorms.

These results clearly indicate that vibration patterns can be used to separate at least two important disturbance types, and that embryos could use fairly simple perceptual or behavioural rules to do so. They also suggest that 'snakes' may be a reasonable category of disturbance, at least in comparison to rain. Since attacks by both *Leptophis ahaetulla* and *Leptodeira annulata* differ from rain in the same ways, it seems unlikely that embryos would need to recognize the disturbance patterns of each species separately.

None the less, distinguishing snakes from rain may not be the most difficult task facing *A. callidryas* embryos. For instance, egg-eating wasps may excite higher-frequency vibrations in egg clutches, and wind may produce low-frequency disturbances of longer duration. Separating all dangerous from all benign disturbances, and assessing

levels of risk in dangerous disturbances, may be more complex than this comparison of rain versus snakes suggests. Also, all of the recordings analysed here were from rigidly mounted clutches, to improve detection of vibrations caused by direct contact with the clutch and minimize vibrations transmitted through the supporting plant structure. The direct-contact vibration patterns will combine with plant-transmitted vibrations, but the extent to which this may improve or hamper distinctions among disturbance types is as yet unknown.

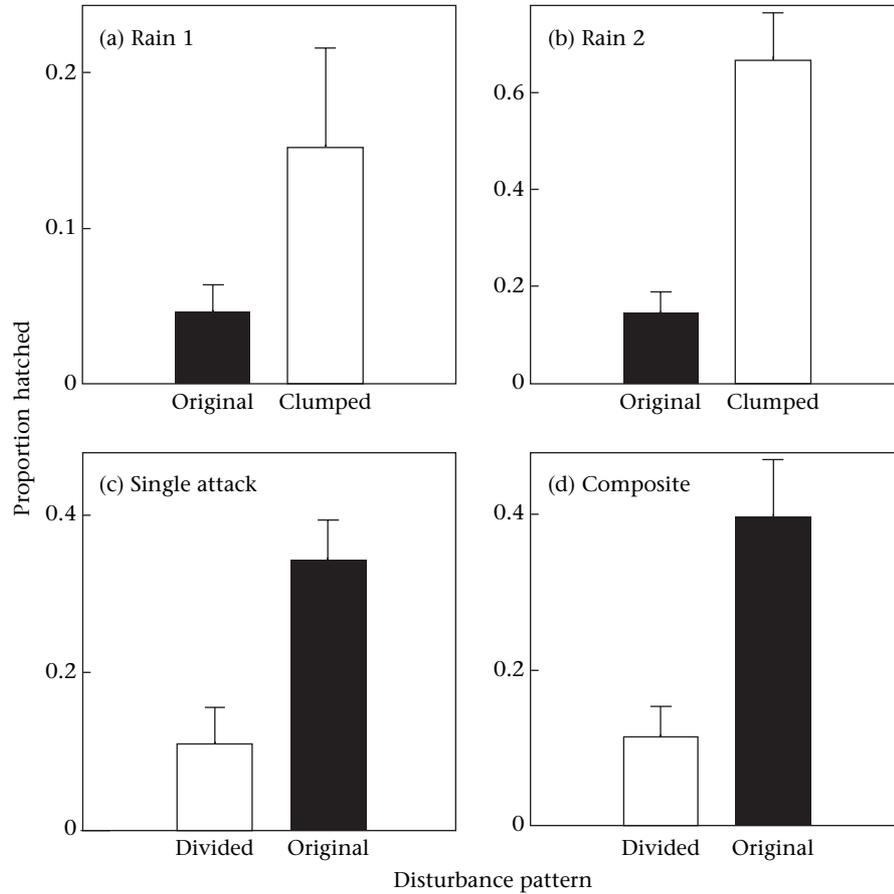
Of course, disturbance types may also differ in other ways, and embryos may use parameters other than those quantified here to distinguish disturbances or assess risk. For instance, snake- and rain-induced vibrations seem also to differ in the shape of their amplitude envelopes. Vibrations elicited by single raindrops start with a high amplitude impact, which is followed by gradually decaying free vibrations. The amplitude modulation of snake vibrations is more variable, depending on the behaviour of the snake, but the peak amplitude is often not at the start of the vibration (personal observations). Embryo movements also produce vibrations, which may provide information to their siblings.

## Playback Experiments

Vibrational cues alone, without any visual or chemical indications of predator attack, can elicit substantial levels of early hatching in *A. callidryas*. Equally important, not all vibrational disturbances elicit hatching. Some vibration playbacks, in which large amounts of energy were introduced into test clutches over periods of several minutes, elicited very little hatching. Thus, embryos clearly distinguish among, and respond differently to, different vibration patterns.

Playbacks of recorded snake attacks elicited substantially more hatching than duration- and amplitude-matched rain sequences. Salient information about the original disturbances was evidently preserved in the recordings, and the embryos responded appropriately to the different stimulus types. Not only did they not need visual or chemical cues to interpret snake vibrations as dangerous, they did not need wetting of the clutch to interpret rain vibrations as safe.

The absolute level of hatching in response to the snake playbacks (Figs 6, 7) was lower than that seen in real snake attacks on the same developmental stage of embryos (70–80%; Warkentin 1995, unpublished data). This may be due to limitations of the playback methods I used. For instance, the amplifier attenuated low frequencies (<40 Hz), which are clearly a major component of snake-induced vibrations. Also, the recorded disturbances used for playback stimuli included both forced-vibration periods, when a snake was actively moving the clutch or a raindrop was impacting the clutch, and the subsequent periods of free vibration of the clutch that follow such external forcing. Thus, for each disturbance event, the playback clutches were moved by the minishaker through the recorded forced and free vibration, plus they showed their own brief period of free vibration after the shaker



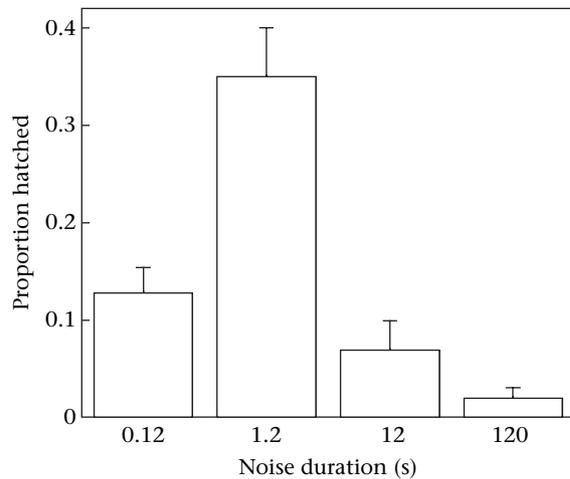
**Figure 7.** Hatching response of *A. callidryas* embryos to playbacks of natural vibration patterns (■) from rainstorms (a, b) and snake attacks (c, d) compared with edited versions (□) of the same sequences, rearranged to clump together raindrops or divide up snake bites (see Fig. 5 for examples of stimuli). In all four cases, stimuli with longer disturbance durations and longer intervals elicited more hatching. Data are means + SE for  $N = 10$  clutches/stimulus.

stopped. This extended the vibration durations and shortened the intervals they experienced, compared to the original recordings. There may be other information, in addition to vibrations, that embryos use to inform their hatching decision. However, the relatively high level of hatching elicited in some vibration playbacks (e.g. Fig. 7b) suggests that vibrations can induce hatching at levels typically seen in snake attacks. Thus, it is plausible that vibrations alone mediate the hatching response to snakes. Clearly, they are an important information source for embryos.

The hatching response to edited snake and rain recordings, and the response to white noise playbacks both indicate that embryos attend to the gross temporal pattern of vibrations (i.e. some aspect of duration, interval and/or cycle duration). Snake attack recordings that originally elicited high levels of hatching were rendered relatively innocuous simply by breaking up the vibrations into shorter bits, separated by shorter intervals. Rain recordings that were originally interpreted as relatively safe elicited substantial hatching after I clumped vibrations from individual drops together, lengthening both the durations of vibrational events and the intervals between them. These manipulations only altered the duration and

spacing of vibrations. Thus, differences in frequency, disturbance period, or total energy are not required to elicit different levels of hatching. Differences in vibration duration and spacing are sufficient for embryos to perceive different levels of risk, at least to the extent that hatching behaviour indicates perception of risk. Furthermore, in all cases, embryos hatched more in response to the more snake-like temporal pattern, and less in response to the more rain-like temporal pattern. Overall, this suggests that two simple characteristics of temporal pattern, disturbance duration and spacing, which clearly differentiate rain and snake vibrations statistically and to a human observer, are also relevant to *A. callidryas* embryos. Embryos may also use frequency information, but frequency differences do not appear necessary to elicit appropriate responses to snake-like and rain-like temporal patterns.

Indeed, embryos showed markedly different hatching responses to bursts of broadband white noise in different temporal patterns, including a strong hatching response to 1.2 s of vibration followed by a 4.8-s interval (Fig. 8). These vibrations bear little resemblance to natural vibrations in many respects. They are not amplitude-modulated, the frequency envelope resembles no natural



**Figure 8.** Hatching response of *A. callidryas* embryos to playbacks of synthetic vibrations based on bursts of 0–11 kHz white noise in a 1:4 ratio to stillness in different cycle durations. Embryos hatched most in response to an intermediate cycle duration of 6 s. Data are means + SE for  $N = 10$  clutches/stimulus.

disturbance, and the pattern is far more precisely repetitive than natural disturbances. Again, the different responses to these stimuli indicate that differences in total energy, peak or RMS amplitude, disturbance to interval ratio, or frequency are not required to elicit different levels of hatching. Differences in cycle duration, vibration duration and/or interval length are sufficient by themselves. Although the white noise stimuli do not match average snake and rain temporal patterns, the highest hatching was elicited by one of the two more snake-like stimuli. The longest cycle duration elicited very little hatching. Indeed, by 2 min into the playback, far more embryos had hatched in the 6-s cycle, having received only 24 s of vibration, than had hatched in the 600-s cycle, where they had then received 120 s of continuous vibration. This suggests that embryos do not perceive more vibration as indicating higher risk. This is congruent with the analysis of vibration patterns, which revealed that the amount of vibration, measured in various ways, is not a good indicator of risk.

### Embryo Behavioural Decisions and Vibrational Information

There is growing evidence that embryos alter hatching timing in response to egg and posthatching risks (e.g. Sih & Moore 1993; Warkentin 1995; Moore et al. 1996; Vonesh 2000; Chivers et al. 2001; Laurila 2002; Wedekind 2002; Johnson et al. 2003). Such responses indicate that embryos are receiving and interpreting information about conditions in their environment. For aquatic amphibian embryos, this information often seems to take the form of chemical cues indicating the presence of predators, although the specific chemicals to which embryos respond are still unknown (Moore et al. 1996; Chivers et al. 2001). Chemical cues can also mediate hatching time of spider

eggs in air (Li 2002). This response is, however, controlled by the egg-guarding mother, not the embryos, suggesting that the adult detects the cues. The terrestrial eggs of California grunion, *Leuresthes tenuis*, hatch in response to mechanical disturbance, in combination with salt water immersion (Griem & Martin 2000), but it is not known how general or specific the mechanical cues are.

For arboreal embryos of red-eyed treefrogs, vibrational cues are clearly important in hatching timing, but only specific patterns of vibrations elicit hatching. Thus, vibrations offer a way to explore the embryos' perceptual space and behavioural decision rules. To understand selection pressures on their perceptual system, it will be necessary to better characterize the vibrational environment of the embryos by recording vibrations from clutches in a broader range of disturbance types and substrate contexts. The responses of embryos to natural and synthetic vibration playback experiments suggest that these will be productive in elucidating the behavioural decisions and perceptual mechanisms of red-eyed treefrog embryos, as acoustic playbacks have been with adult anurans and other taxa (McGregor 1992).

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