



## Articles

## Is it safe? Red-eyed treefrog embryos assessing predation risk use two features of rain vibrations to avoid false alarms

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Prey use predator cues to inform defensive decisions. Detecting these cues is often complicated by benign stimuli that resemble and can be mistaken for predators, leading prey to display costly defences incorrectly. One strategy that prey have evolved to reduce these ‘false alarms’ is to respond only to stimuli with characteristics consistent with predator cues. Decision errors might still be frequent, however, in cases where the probability distributions of benign stimulus properties completely overlap those of predator cues. In such cases, inhibition of defensive responses by characteristic features of benign stimuli could further improve discrimination. Red-eyed treefrog embryos, *Agalychnis callidryas*, hatch prematurely to escape egg predators. They detect predators using vibrations generated during attacks. However, common benign disturbances such as rainstorms generate vibrations with property probability distributions that largely overlap those of predators. We used vibration playbacks to test the hypotheses that embryos use two features of rainstorm vibrations not shared by predator attacks, characteristic high frequencies and an initial period of intensity buildup, to avoid hatching in response to this benign stimulus. The escape-hatching response to otherwise stimulatory vibrations is reduced in the presence of either feature characteristic of rainstorms. Either *A. callidryas* embryos use rainstorm features to inform their hatching decision or these features alter their perception of predator cues. Identifying likely sources of potential false alarms and comparing their stimulus characteristics to predator cues and prey decision rules will improve our understanding of both the information processing challenges facing prey and the ways they solve them.

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Many prey use cues generated by predators to inform decisions about when to initiate defensive behaviours. The evolution of these defensive strategies is shaped by two types of decision errors. Failure to respond appropriately to stimuli indicative of risk, ‘missed cues’ in detection theory, is often fatal. Similarly, responding defensively to benign-source stimuli, ‘false alarms’, can result in lost foraging time, lost opportunities to mate, or unnecessary exposure to other predators (Lima & Dill 1990). A substantial body of research addresses the sensory modalities and specific features of predator cues used by prey to assess risk (e.g. Kats & Dill 1998; Blumstein et al. 2000; Djemai et al. 2001; Stankowich & Blumstein 2005). Much less work has addressed how common

benign stimuli, potential sources of false alarms, influence the defensive strategies used by prey.

For prey that rely on incidental cues generated by predators to inform defence, avoiding false alarms is not a trivial task. Unlike communication signals, incidental cues have not evolved to transfer information unambiguously (Guilford & Dawkins 1991; Endler 1992). Thus, their properties (peak frequency, amplitude, etc.) often have broad and variable probability distributions that can overlap with those of benign stimuli (Bacher et al. 1996; Casas et al. 1998; Warkentin 2005; Caldwell et al. 2009). Such similarity may be particularly likely for vibrational and acoustic stimuli because they are strongly affected by the physical properties of the vibrating structures that produce and propagate them, regardless of the original source of excitation (Ginsberg 2001). Thus the sound of rustling grass moved by a stalking leopard or a grazing gazelle and vibrations in a leaf impacted by a raindrop or a landing insect will have similarities due to the mechanics of the vibrating plant. In addition, selection for crypsis works to further reduce the separation between stimuli from predator and benign sources.

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Although many benign stimuli, such as incidental predator cues, are nonstereotyped in form, they do have statistical regularities that result in characteristic property probability distributions that could aid in discrimination (e.g. Barth et al. 1988; Casas et al. 1998; Castellanos & Barbosa 2006; Caldwell et al. 2009). The contrasts between property distributions of predator cues and those of relevant benign-source stimuli define the axes of variation that function to discriminate these stimulus types (Macmillan & Creelman 2005).

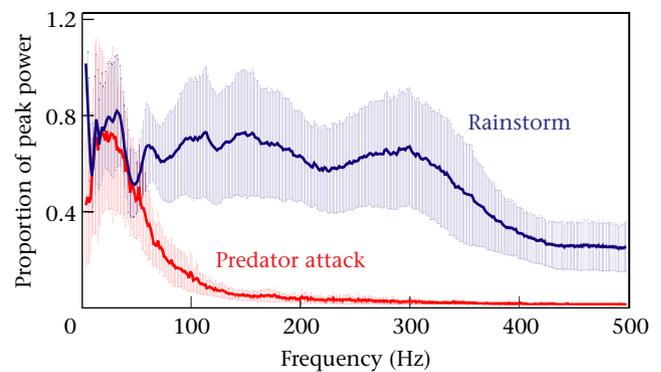
To better understand prey defensive decisions it is, therefore, necessary to characterize both predator cues and potential sources of frequent false alarms to identify stimulus features that might be used for discrimination. This is a standard technique used for studying discrimination in communication contexts (e.g. Nelson & Marler 1990; Chittka & Thomson 2001; Wollerman & Wiley 2002). By contrast, research on predator–prey interactions has focused almost exclusively on the detection of predator cues, with less explicit consideration of environmental stimuli that lead to false alarms or of decision rules that prey use to avoid these errors.

## STUDY SYSTEM AND HYPOTHESES

We examined the role that characteristics of benign vibrational stimuli play in the escape-hatching decision of red-eyed treefrog, *Agalychnis callidryas*, embryos. Red-eyed treefrogs inhabit wet forests from the Yucatan to northern Colombia (Duellman 2001), and lay gelatinous egg clutches on vegetation overhanging ponds. Undisturbed embryos usually hatch after 6–7 days in Panama, but are capable of hatching as early as 4 days to escape arboreal egg predators, such as snakes and wasps, by dropping to the pond below (Warkentin 1995, 2000a). On average, snake-induced hatching begins 16 s after the start of attacks, and embryos have all hatched or been eaten within 5 min (Warkentin et al. 2007). Escape hatching is cued by vibrations excited within clutches by snakes, and vibration may cue hatching in response to other predators as well (Warkentin 2005). Several common benign disturbances, including wind, routine movements of embryos within their eggs and rainstorms, also excite vibrations in clutches. The amplitude, frequency and temporal properties of these predator and benign-source vibrations are highly variable and have broad, overlapping distributions (Warkentin 2005; Caldwell et al. 2009).

Rainstorms may be particularly difficult to discriminate from predator disturbances. Rain excites strong egg clutch vibrations at all frequencies excited by predator attacks (Fig. 1), and in many storms the dominant frequency is indistinguishable from the mean dominant frequency of attacks (Caldwell et al. 2009). Moreover, rain can excite vibrations of greater peak and root-mean-square acceleration than those recorded during snake attacks (Warkentin 2005; Caldwell et al. 2009).

Nevertheless, discrimination between predator and rain vibrations is critical, because rainstorms are common and false alarms are costly. In Corcovado Park, Costa Rica, our field site where snake predation is highest, snakes attacked ~20% of clutches during the 2-day period when embryos were hatching-competent but still premature, and mortality of embryos that failed to hatch was near 100% (Warkentin 1995; Gomez-Mestre & Warkentin 2007). In our least rainy field site, Gamboa, Panama, the likelihood of eggs being rained on during this same developmental period was approximately 80% (Warkentin & Caldwell 2009). Embryos hatching early face increased risk of predation from several species of aquatic predators. Actual mortality varies with conditions in the pond but is typically intermediate between that of hatching-competent embryos in undisturbed clutches and that of embryos that fail to hatch under attack. In 24 h laboratory trials with different



**Figure 1.** Average relative distribution of energy across frequencies for vibrations in *A. callidryas* egg clutches during predator attacks (snakes: *Leptodeira annulata*,  $N = 17$ ; *Leptodeira septentrionalis*,  $N = 11$ ; *Leptophis ahetulla*,  $N = 13$ ; wasp: *Polybia rejecta*,  $N = 18$ ) and rainstorms ( $N = 19$ ), plotted on a quadratic scale. Shown are means of individual clutch disturbances, standardized to peak power, and 95% confidence intervals. Predator attacks excite frequencies below 100 Hz. Rainstorms also excite energy within this range, but excite a range of higher frequencies as well. Higher frequencies may be used by *A. callidryas* embryos to identify rainstorm vibrations. A more complete description of vibration frequencies excited by each type of clutch disturbance is presented elsewhere (Caldwell et al. 2009).

predators and habitat structures, 10–86% of prematurely hatched tadpoles were eaten (Warkentin 1995). Although multiple predators, pathogens and flooding can kill *A. callidryas* eggs, these risks also cue hatching, and survival of undisturbed eggs through the plastic hatching period is usually 100% (Warkentin 1995, 2000b).

In fact, embryos rarely hatch prematurely during rainstorms (Warkentin 1995; Caldwell et al. 2009). We have previously demonstrated that embryos integrate both temporal (Warkentin 2005; Warkentin et al. 2006) and frequency (Caldwell et al. 2009) information into their vibration-cued hatching decision. A relatively narrow range of vibration duration and interval patterns stimulate hatching (Warkentin 2005; Warkentin et al. 2006). In addition, energy must be present at frequencies below approximately 150 Hz to elicit hatching, with the strongest hatching response to lower frequencies within this range, consistent with the spectra of predator vibrations (Fig. 1) (Caldwell et al. 2009). Higher frequencies and other temporal patterns elicit little or no hatching. These criteria, however, appear insufficient to consistently prevent hatching during rainstorms. Comparing clutch vibrations recorded during predator attacks and rainstorms suggests two additional properties that embryos could use to further refine their hatching response (Warkentin 2005; Caldwell et al. 2009).

We used playback experiments to test whether a characteristic frequency feature of rainstorms or characteristic vibrations at the start of rainstorms contribute to the relative lack of hatching in response to this benign stimulus. Rain excites energy at higher frequencies than do predator attacks, up to 600 Hz (Fig. 1; Caldwell et al. 2009). We hypothesized that the hatching response to low frequencies is reduced when these higher frequencies typical of rainstorms are also present. Similarly, while both predator attacks and rainstorms excite high-amplitude vibrations within clutches, the most intense rain vibrations are typically preceded by lower-amplitude vibrations that gradually increase in intensity. By contrast, although snake attacks sometimes begin with a few low-amplitude tongue flicks, high-amplitude attack vibrations are often preceded by vibrational silence (M. S. Caldwell, A. T. D'Amato, J. G. McDaniel & K. M. Warkentin, unpublished data). We hypothesized that the period of low-intensity vibrations at the start of rainstorms reduces the embryos' hatching response to subsequent, more intense vibrations.

## METHODS

### *Clutch Collection and Care*

We collected newly laid *A. callidryas* egg clutches, with the leaves on which they were laid, from Ocelot Pond, 2 km south of Gamboa, Panama. We brought clutches to an open-air laboratory in Gamboa, removed any dead eggs or debris, trimmed excess leaf area as necessary, and taped them by the remaining leaf area to plastic cards in preparation for recording or playback. We placed clutches over water and misted them several times a day with rainwater to prevent desiccation. Following playbacks all hatched tadpoles were returned to Ocelot pond. This research was conducted under permits from the Panamanian National Environmental Authority (Autoridad Nacional del Ambiente). Research protocols were approved by the Smithsonian Tropical Research Institute and the Boston University Institutional Animal Care and Use Committee (Protocols 02-013 and 05-022).

### *Vibration Recordings*

Recording methods followed Caldwell et al. (2009). To collect recordings of vibrations excited within clutches during rainstorms, which we used for natural stimulus playbacks, we inserted miniature accelerometers (0.2 g, Endevco 25B, Endevco Corp., San Juan Capistrano, CA, U.S.A.; 0.14 g, AP Technology AP19, AP Technology International, Oosterhout, The Netherlands) into the jelly of hatching-competent egg clutches. We then exposed these clutches to unobstructed rain and recorded the resulting vibrations. Accelerometers were powered by signal conditioners (Endevco 4416B; AP Technology APC7), and signals were digitized with an Onkyo MSE-U33HB sound card (Onkyo USA Corp., Upper Saddle River, NJ, U.S.A.). All recordings were made using Canary bioacoustics software (v.1.2.4, Cornell Lab of Ornithology, Ithaca, NY, U.S.A.) at 22.1 kHz on a Macintosh G4 notebook computer.

### *Vibration Playback Experiments*

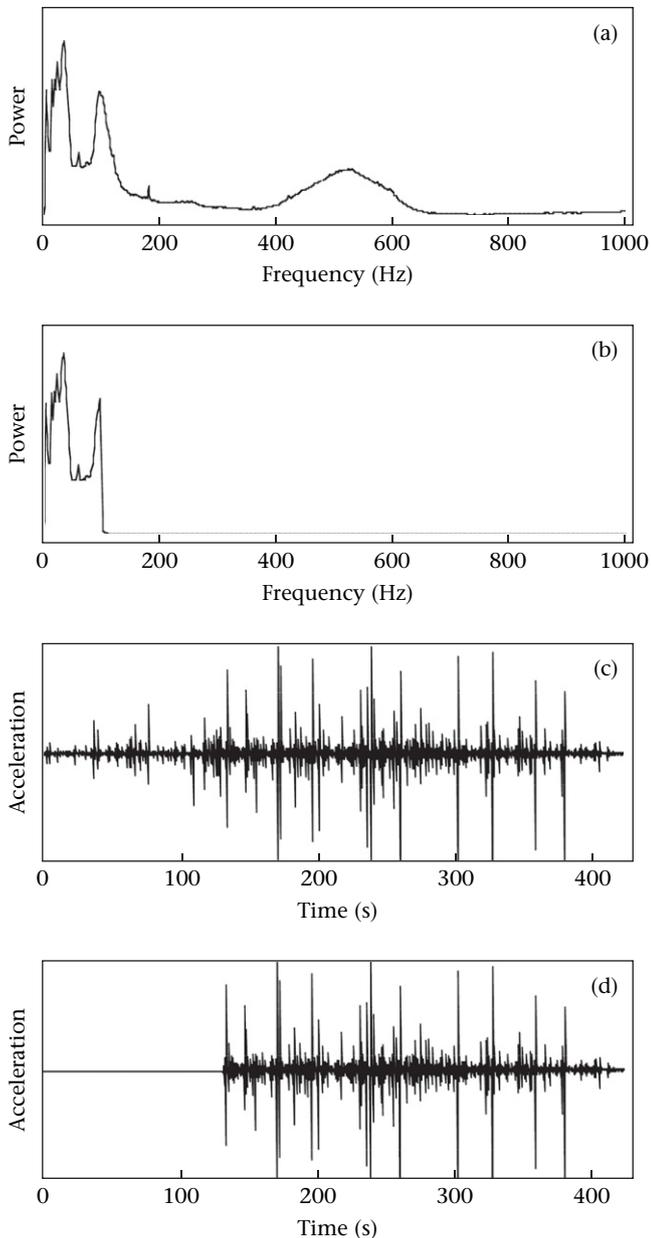
We conducted three playback experiments to test whether two characteristic features of vibrations excited by rainstorms contribute to the relative lack of hatching in response to these benign stimuli. For all three experiments, methods followed those of Warkentin et al. (2006), and differed only in the stimuli presented. Vibrational stimuli were played from Canary on a Macintosh G4 laptop computer, output via an external sound card (MSE-U33HB) and a custom-made amplifier (E. Hazen, Boston University Electronic Design Facility), and transduced using an electrodynamic minishaker (model 4810; Brüel & Kjær, Nærum, Denmark). Each clutch was mounted on a rigid support stand. We coupled shaker movements with the egg clutch using blunt metal tines at the end of a rigid stinger, inserting the tines into the clutch jelly between eggs. We only used clutches containing at least 20 eggs. Five minutes after any hatching induced during set-up, we noted and removed any hatched tadpoles. If 25% or more of a clutch hatched during set-up, we did not use it for the experiment. During playback, clutches were vibrated vertically, and any hatchlings fell into a tray of water. We recorded the number of hatched tadpoles every minute throughout the duration of the playback stimulus and for an additional 5 min thereafter. Following this monitoring period, we assessed the hatchability of any remaining embryos using manual stimulation; thus, each clutch was exposed only to one stimulus.

Two playback experiments tested the effect of high-frequency vibrations, characteristic of rainstorms, on the embryo hatching response. In the first, we used two synthetic stimuli. One stimulus consisted of bursts of band-limited noise (range 0–100 Hz;  $N = 6$ ),

played in a temporal pattern (1 s duration, 1 s interval) and at a peak amplitude ( $30 \text{ m/s}^2$ ) that elicited a moderate level of hatching (mean  $\pm$  SE =  $36 \pm 0.03\%$ ,  $N = 79$ ) in a previous study (Warkentin et al. 2006). The other stimulus consisted of 0–500 Hz noise in the same temporal pattern ( $N = 9$ ). We adjusted the amplitude of this 0–500 Hz stimulus such that its intensity over the 0–100 Hz range matched that of the first stimulus. Thus, it essentially included the other stimulus plus additional energy at higher frequencies. To construct stimuli, white noise was generated in SoundEdit16 (V.2, Macromedia, San Francisco, CA, U.S.A.), low-pass filtered in Canary, and then divided into 1 s bursts at zero crossings. Because of frequency-dependent filtering in our playback apparatus, higher frequencies were played at slightly lower amplitudes. This filtering affected the 0–100 Hz range of each stimulus equally. These two stimuli were presented over 5 nights as part of a larger playback experiment. Stimuli from this larger set were played in random order. The availability of egg clutches was limited, however, and unequal numbers of the 0–100 Hz and 0–500 Hz stimuli were presented on some nights. In previous experiments we have found very little temporal variation in overall hatching patterns (Warkentin et al. 2006; Caldwell et al. 2009).

Clutch vibrations excited by rainstorms are far more complex than the synthetic stimuli used in our first experiment, varying widely in temporal pattern, amplitude and other properties (Warkentin 2005; Caldwell et al. 2009). To test whether the presence of high frequencies reduces hatching in response to natural rainstorm vibrations, in our second experiment we played embryos five exemplars of clutch vibrations excited by rainstorms, and the same exemplars low-pass filtered in Canary to remove frequencies above 100 Hz ( $N = 10$ –13 for each exemplar/treatment combination; Fig. 2a). Although raindrop frequency spectra are highly variable, most raindrops excite broadband energy, and filtering altered the temporal properties of rain recordings very little. Rain exemplars each contained a natural buildup in intensity, lasting a minimum of 1 min but not more than 3 min in length, followed by 5 min of intense rain. Stimuli were equalized using custom scripts in MatLab (R13, MathWorks, Natick, MA, U.S.A.) to correct for frequency filtering in our playback apparatus, and playback fidelity was checked by rerecording. In rainstorms the mean  $\pm$  SD intensity ratio of energy below 100 Hz to energy above 100 Hz is  $0.49 \pm 0.20$  ( $N = 19$  rainstorms). The average ratio of energies in the rain exemplars used in the filtered rain experiment was similar ( $0.46 \pm 0.45$ ,  $N = 5$  stimuli). All rainstorm exemplars had dominant frequencies below 100 Hz, and the dominant frequencies of stimuli were not affected by filtering. Although few embryos hatch prematurely in response to rainstorms in the field (Warkentin 1995; Caldwell et al. 2009), it would be difficult to quantify the effects of variation in rainstorm properties if the full-spectrum stimuli produced essentially no hatching. We, therefore, adjusted the amplitude of each unfiltered stimulus to elicit approximately 15% hatching during pilot testing. The resulting stimuli were 3–10 times higher in peak amplitude than the original recordings, but were within the amplitude range of rainstorms that we have recorded from egg clutches in Panama (Warkentin 2005), and elicited far less hatching than snake attack vibrations do when played at the same amplitude (M. S. Caldwell, J. G. McDaniel & K. M. Warkentin, unpublished data). For each exemplar, filtered and unfiltered stimuli were presented in random order to pairs of clutches.

The period of less intense vibrations characteristic of the start of rainstorms may also reduce the hatching response to more intense vibrations that follow. To test this, in our third experiment, we played embryos five exemplars of recorded rain vibrations, and the same exemplars without their initial periods of increasing intensity ( $N = 8$ –10 for each exemplar/treatment combination; Fig. 2b). Four



**Figure 2.** Examples of vibration playback stimuli based on a rainstorm recording. (a) Distribution of energy across frequencies for an unfiltered rainstorm vibration exemplar used during playback. (b) Power spectrum for the same exemplar filtered to remove energy above 100 Hz. Both spectra are plotted on a quadratic scale. (c) Waveform depicting clutch vibrations excited during a rainstorm, including initial period of intensity buildup. (d) Waveform for the same storm after the period of initial intensity buildup has been removed. All stimuli (a–d) were modified from the same rainstorm vibration exemplar, C723.

of these exemplars were also used in the filtered rain experiment. Again, periods of intensity buildup ranged from 1 to 3 min in duration, and intense periods of rain were 5 min in duration. To allow us to better quantify the effects of the initial lower-intensity periods of rainstorms, we adjusted the amplitude of complete rain stimuli, including this initial period, to elicit approximately 15% hatching in pilot testing as above. For each exemplar, stimuli with and without the period of buildup were presented in random order to pairs of clutches. Although the initial vibrations produced by rainstorms have characteristically low peak acceleration amplitude, the temporal or frequency properties of this period may also affect

embryo behaviour. Thus, our experiment did not test embryo response to amplitude modulation per se, but rather embryo response to the presence of vibrations recorded from the start of rainstorms.

#### Statistical Analyses

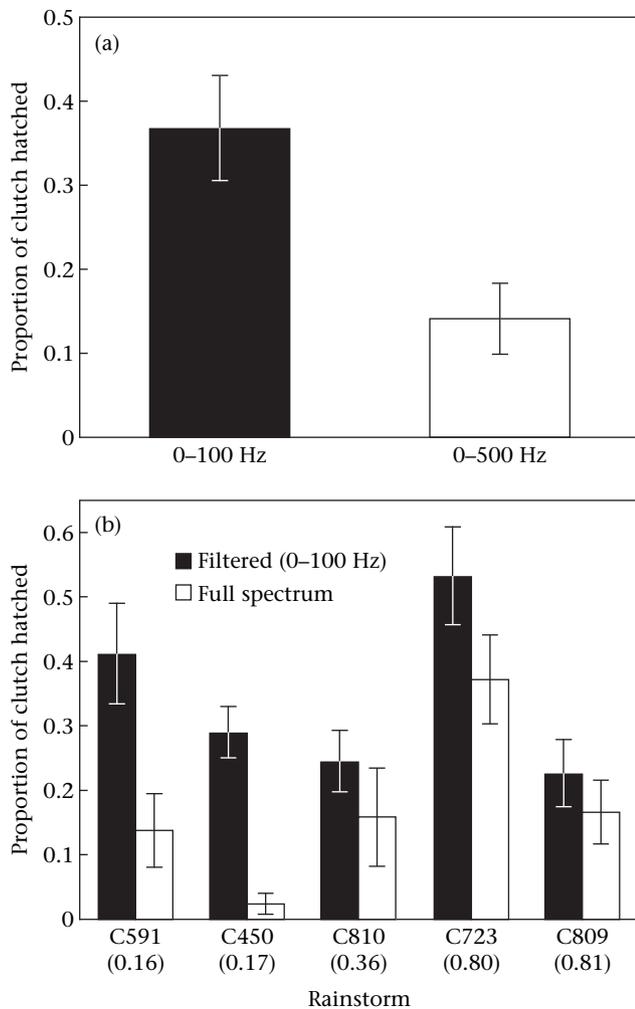
We compared the proportions of embryos within a clutch that hatched in response to synthetic stimuli varying in the presence of high-frequency energy using a Mann Whitney  $U$  test in SPSS (v.16, SPSS Inc., Chicago, IL, U.S.A.). The patterns of hatching in experiments using edited rainstorm exemplars to test the effects of high frequencies and the period of increasing intensity at the start of rainstorms were overdispersed and positively skewed. These data fit negative binomial distributions with log-link functions and were analysed using generalized linear models (GzLM) in SPSS, testing for effects of experimental treatment, exemplar, and their interaction. The ancillary dispersion parameter for these tests,  $k$ , was estimated by the software. There is a large amount of variation between rainstorms in their frequency distributions (Caldwell et al. 2009). We used Spearman's  $r_s$  to test for a correlation between the ratio of low- to high-frequency energy and any change in mean hatching response to rainstorm exemplars caused by removing high-frequency energy.

#### RESULTS

In all three experiments, removing energy from the vibrational stimulus increased the hatching response. A higher proportion of embryos hatched in response to the synthetic stimulus limited to 0–100 Hz than to the broader-band 0–500 Hz stimulus (Mann–Whitney  $U$  test:  $U = 4.0$ ,  $N_1 = 6$ ,  $N_2 = 9$ ,  $P = 0.005$ ; Fig. 3a). Similarly, the hatching response to playback of rain recordings increased when energy above 100 Hz was removed (GzLM:  $\chi^2_1 = 23.0$ ,  $P < 0.001$ ; Fig. 3b). Removing the natural initial period of buildup in the intensity of vibrations at the start of rainstorms also increased the hatching response to succeeding more intense rain vibrations ( $\chi^2_1 = 33.9$ ,  $P < 0.001$ ; Fig. 4). Hatching varied with rainstorm exemplar both in playbacks testing the effects of high-frequency vibrations on hatching ( $\chi^2_4 = 38.6$ ,  $P < 0.001$ ) and in playbacks testing the effect of the initial period of intensity buildup ( $\chi^2_4 = 36.8$ ,  $P < 0.001$ ). There was a significant interaction effect between rainstorm exemplar and the presence of high-frequency energy ( $\chi^2_4 = 12.7$ ,  $P = 0.013$ ), but no such interaction between rainstorm exemplar and the presence of the initial period of rainstorm ( $\chi^2_4 = 2.1$ ,  $P = 0.714$ ). The ratio of low to high frequencies in each rain exemplar was significantly correlated with the change in hatching that resulted from low-pass filtering stimuli (Spearman rank correlation:  $r_s = -0.90$ ,  $N = 5$ , one-tailed  $P = 0.019$ ).

#### DISCUSSION

Red-eyed treefrog embryos use duration, interval and frequency properties of vibrational cues to assess egg predation risk. If the value of any of these properties is inconsistent with predator attack, embryos do not hatch, but none alone can rapidly and reliably eliminate rain as a potential source of the cue (Warkentin 2005; Warkentin et al. 2006; Caldwell et al. 2009). Such ambiguity may be a common problem for prey using incidental vibrational or acoustic cues to assess risk, both because predators are often under selection for crypsis and because the properties of all vibrations, regardless of source, partly reflect the mechanics of the vibrating structure (Ginsberg 2001; Caldwell et al. 2009). Red-eyed treefrog embryos overcome this by combining information from multiple cue properties (Warkentin et al. 2006; Caldwell et al. 2009) and by sampling

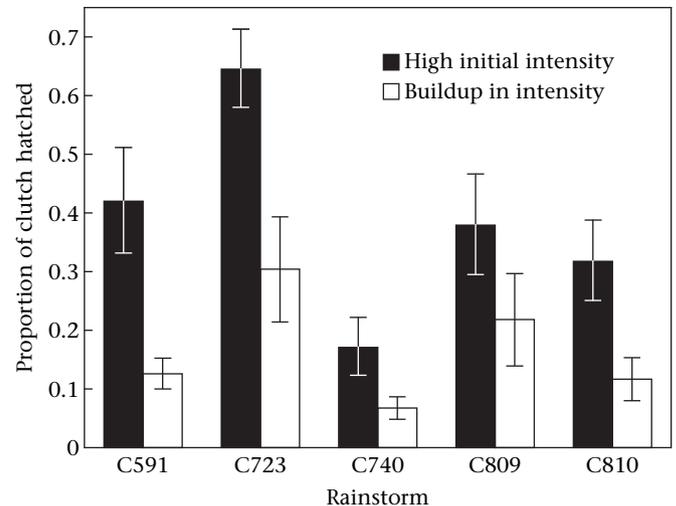


**Figure 3.** Effect of high-frequency vibrations, characteristic of rainstorms, on *A. callidryas*' escape-hatching response. (a) Embryos were played bursts of synthetic 0–100 Hz band-limited white noise with ( $N = 6$ ) and without ( $N = 9$ ) additional high-frequency energy (100–500 Hz). (b) Embryos were played full-spectrum rainstorm vibrations from five rainstorm exemplars and those same exemplars filtered to remove energy above 100 Hz. For each exemplar, the ratio of energy below 100 Hz to energy above 100 Hz is provided in parentheses.  $N = 10$ –13 for each exemplar  $\times$  treatment combination. Data are means  $\pm$  SE.

relatively long periods of vibrations to exploit statistical regularities in the absence of categorical differences (Warkentin et al. 2007). Here we show that, in addition, the hatching response is inhibited by two vibrational features that distinguish rainstorms, a common benign disturbance and potential source of false alarms, from predator attacks: high-frequency energy and initial periods of building intensity.

#### Influence of High-frequency Rain Vibrations

Red-eyed treefrog embryos do not hatch in response to high frequencies characteristic of rainstorms when these are played in isolation (Caldwell et al. 2009). This pattern is not due to an inability of the embryos to sense this energy. Instead, high frequencies reduce the response to stimuli that would otherwise elicit higher levels of hatching. The proximate mechanism underlying this adaptive response is not clear. Embryos may use the presence of high-frequency energy to identify strong vibrational stimuli as benign. Alternatively, high-frequency vibrations may partially mask the perception of stimulus characteristics that would



**Figure 4.** Effect of the period of natural buildup in the intensity of vibrations at the start of rainstorms on *A. callidryas*' escape-hatching response to subsequent intense rain vibrations in playbacks of five rainstorm exemplars.  $N = 8$ –10 for each exemplar  $\times$  treatment combination.

otherwise elicit hatching. Both peripheral (energetic masking) and complex higher-level masking phenomena are well documented in anurans (Narins et al. 2006). There was a significant trend towards stronger hatching inhibition in rain exemplars with relatively more high-frequency energy (Fig. 3b), which is equally consistent with both potential mechanisms. The dominant frequencies of vibrations excited by most rainstorms are in the range of those excited by egg predators, below 100 Hz, and the range of high frequencies characteristic of rainstorms does not overlap the range that stimulates hatching (Caldwell et al. 2009). These factors reduce the likelihood that high frequencies are operating as a masker (Gelfand 2004), but further research into sensory physiology of *A. callidryas* embryos will be necessary to resolve this question.

#### Influence of Initial Periods of Low-intensity Vibration in Rainstorms

Our playback results are also consistent with the hypothesis that embryos use some feature of the period of intensity buildup at the start of rainstorms to identify disturbances as benign. While this period is characteristically of lower amplitude than later vibrations excited by the same storms, amplitude differences per se are not necessarily responsible for reduced hatching. The start of rainstorms may also have characteristic temporal pattern or frequency features that are informative to embryos. Indeed, the temporal pattern of vibrations in this initial, lighter rain is almost certainly perceived as different from later, more intense, rainstorm vibrations (Warkentin et al. 2006). Again, the proximate mechanism of inhibition is not clear. Embryos may have evolved a specific response to features at the start of vibrational stimuli, or our playback results may be explained by more general perceptual phenomena. Behavioural habituation or sensory adaptation could account for the pattern of reduced hatching that we observed when the intensity buildup at the start of rainstorms was present. These phenomena are well documented to affect stimulus detection and discrimination in both the psychophysics and the communication literatures (Hinde 1970; Narins et al. 2006).

#### Implications for Embryo Escape-Hatching Decisions

Whether additional energy interferes with the perception of stimulatory vibrations, or embryos evolved to integrate information

from vibration features indicative of rain into their hatching decision, the end result is the same: *A. callidryas*' hatching response is refined such that embryos are less likely to hatch prematurely during intense, but benign, tropical storms and less likely to be killed by aquatic predators as a result. This inhibition of the escape-hatching response presumably contributes to the low level of premature hatching during rainstorms in nature (Warkentin 1995; Caldwell et al. 2009). Moreover, even if hatching inhibition is a fortuitous consequence of *A. callidryas*' sensory physiology, escape hatching is modulated by vibrational features indicative of rainstorms, a common benign disturbance and potential source of false alarms, and embryos are therefore exposed to selection on their responses to these features.

#### Understanding Prey Strategies for Avoiding False Alarms

Substantial attention has been focused on the nature of predator cues and how prey use these to make decisions about defence (e.g. Blumstein et al. 2000; Djemai et al. 2001; Stankowich & Blumstein 2005). Characterizing the features of predator stimuli that prey use to cue defensive responses elucidates part of their risk assessment strategies: how they avoid missed cues. Costly false alarms, however, also shape prey defensive strategies. While some environmental stimuli are unlikely to elicit inappropriate defensive responses (i.e. benign stimuli with property probability distributions that do not overlap those of predator cues), others may be more difficult to discriminate from indicators of risk. If common benign stimuli have property distributions that substantially overlap those of predator cues, a more complex risk assessment strategy may be required. Features characteristic of the benign stimuli (e.g. energy in certain frequency ranges) that are absent from predator cues define additional informative properties, or axes of variation, that may refine prey responses to other features consistent with risk. Identifying and characterizing likely sources of potential false alarms is necessary to determine the extent to which prey decision rules are shaped by characteristics of benign stimuli and how prey avoid false alarms.

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