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Flexible information sampling in vibrational assessment of predation risk by red-eyed treefrog embryos

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Summary

Prey assessing risk may miss cues and fail to defend themselves, or respond unnecessarily to false alarms. Error rates can be ameliorated with more information, but sampling predator cues entails risk. Red-eyed treefrogs have arboreal eggs and aquatic tadpoles. The embryos use vibrations in snake attacks to cue behaviorally mediated premature hatching, and escape, but vibrations from benign sources rarely induce hatching. Missed cues and false alarms are costly; embryos that fail to hatch are eaten and hatching prematurely increases predation by aquatic predators. Embryos use vibration duration and spacing to inform their hatching decision. This information accrues with cycles of vibration, while risk accrues over time as snakes feed. We used vibration playback experiments to test if embryos adjust sampling of information based on its cost, and measured latency to initiate hatching in videotaped snake attacks. Embryos did not initiate hatching immediately in attacks or playbacks, and the delay varied with the rate at which information accrued. Embryos started hatching sooner in response to stimuli with shorter cycles but sampled fewer cycles (less information) of longer-cycle stimuli before hatching. This flexible sampling is consistent with embryos balancing a trade-off between the value and cost of information.

Key words: hatching, predator detection, playback, prey uncertainty, seismic, vibration, *Leptophis ahaetulla*, *Leptodeira annulata*, *Agalychnis callidryas*.

Introduction

Predator- and pathogen-induced shifts in the size and developmental stage at which animals hatch are broadly distributed among vertebrates [e.g. amphibians (Sih and Moore, 1993; Warkentin, 1995), fishes (Kusch and Chivers, 2004; Wedekind, 2002), reptiles (Moreira and Barata, 2005)] and have probably evolved multiple times. Some embryos respond to chemical cues (e.g. Chivers et al., 2001; Johnson et al., 2003) and others to vibrational cues from predators (Warkentin, 2005). These responses provide a natural context in which to examine the sensory and information-processing capacity of embryos. We examined information sampling by frog embryos that use substrate-borne vibrations to cue behaviorally mediated premature hatching.

Risk assessment is critical for inducible defenses (Tollrian and Harvell, 1999) and requires that animals distinguish predator cues from benign-source stimuli (noise). This is fundamentally a signal detection problem (Bradbury and Vehrencamp, 1998; Macmillan and Creelman, 2005). For any cue property that an animal could assess, overlap is likely between the value of that property in predator cues and noise. Such overlap occurs in communication signals selected to be conspicuous (Endler, 1992) and is likely greater for cues from predators or prey selected for crypsis (Getty and Krebs, 1985; Wilcox et al., 1996). Thus, any criterion used to distinguish predator cues will result in errors, including false alarms (unnecessary defense) and/or missed cues (failure to defend). The criterion may be adjusted depending on the cost of each error type, but there is a trade-off. For instance, the criterion may be relaxed to minimize fatalities from missed cues; however, this increases the incidence of false alarms. Strong selection against both missed cues and false alarms should favor sampling strategies that accept additional costs in order to improve accuracy of risk assessment. Prey could use more information to ameliorate the trade-off in two ways. (1) They could assess multiple, independent properties of predator cues simultaneously. Overlap with noise should decrease with each property added, but the required neural processing likely increases as well. (2) They could base their response on a larger sample of the cue property. Increased sampling improves the precision of estimates, potentially reducing overlap. However, if a hunting predator is the source of cues, increased sampling before defense increases risk.

We examined information sampling by frog embryos that use substrate-borne vibrations to assess predation risk. Vibrational sensitivity is evolutionarily ancient and phylogenetically widespread (Hill, 2001), and a diverse range of prey use vibrations to cue antipredator behavior (Tautz and Markl, 1978; Bacher et al., 1997; Burger, 1998; Warkentin, 2005; Castellanos and Barbosa, 2006). Some show immediate defensive responses to vibrations, and the behaviors involved, such as ceasing to call (Lewis and Narins, 1985; Narins, 1990), freezing (Burger, 1998) or changing posture (Gnatzy and Kämper, 1990), appear low cost. In these cases, response criteria may have been relaxed to reduce missed cues and, if so, we expect high false alarm rates, i.e. defensive responses to non-predator vibrations. There may also be a selective premium on response speed, if risk increases steeply with sampling time prior to defense. If so, the cue properties used should be amenable to rapid assessment, e.g. frequency or amplitude. Assessing larger-scale temporal properties requires more time and, in the case of predator vibrations, more risk, although temporal properties of vibrations appear more robust to degradation than frequency properties and more important in intraspecific communication (Michelsen et al., 1982; Randall, 1995; Hill, 2001; Virant-Doberlet and Cokl, 2004).

Study system

Red-eyed treefrogs, *Agalychnis callidryas* Cope 1862, lay eggs on vegetation over ponds and swamps, and tadpoles fall into the water upon hatching. Embryos hatch as much as 30% prematurely – both earlier and less developed – to escape from egg-eating snakes, wasps and other dangers (Warkentin, 1995; Warkentin, 2000; Warkentin et al., 2001; Warkentin, 2002). Although in many animals hatching is a slower and largely enzymatic process (Carroll and Hedrick, 1974; Yamagami, 1981; De Vries and Forward, 1991), in *A. callidryas*, as in some other frogs and fishes (Brown and Iskandar, 2000; Griem and Martin, 2000), hatching is a rapid behavioral process. Hatching is also an irreversible life-stage transition that exposes hatchlings to a new suite of aquatic predators. Premature hatchlings are substantially more vulnerable than full-term hatchlings to aquatic predators (Warkentin, 1995; Warkentin, 1999a). Thus, the cost of false alarms is high and, as with missed cues, exacted as increased mortality.

Escape hatching can be induced by vibrations recorded from snake attacks (Warkentin, 2005), and two temporal properties, vibration duration and interval or spacing, affect the hatching response (Warkentin et al., 2006b). Since assessing temporal properties requires time and entails risk, we asked two questions: (1) how much time do *A. callidryas* devote to sampling vibrational cues before hatching and (2) do they use a fixed or flexible sampling strategy? Information from duration and interval properties accrues with cycles of vibration and silence. Thus, a given time sample contains more of such information if cycles are short rather than long. By contrast, risk appears to accrue with time, not vibration cycles, as snakes consume eggs (K.M.W. and A.T.D., manuscript in preparation). Embryos might use a fixed sampling rule, for instance based on a time period, number of vibrations or simply amount of stimulation. Alternatively, they might balance the potential cost of sampling with the value of information, adjusting sampling period with the rate at which information accrues. To assess sampling, we compared the time course of hatching for eggs exposed to vibrational stimuli that elicit similar levels of hatching (Warkentin et al., 2006b) but differ in cycle length, i.e. the rate at which temporal pattern information accrues. We also examined videotapes of snake attacks on egg clutches to assess the latency of hatching and duration of attacks.

Materials and methods

Vibration playback experiment

We compared the time course of hatching in response to four rhythmic vibrational patterns consisting of bursts of 0–100 Hz white noise separated by intervals of silence (Fig. 1A). The patterns were chosen to elicit similar levels of hatching, based on prior results (Warkentin et al., 2006b), but differ across an order of magnitude in cycle length (= vibration duration + interval), while holding duty cycle (= vibration duration/cycle length) and total energy constant. Vibrations had approximately rectangular amplitude envelopes and were matched for peak acceleration. Stimuli were played to egg clutches for 5 min, during which we counted the number of hatched embryos every 10 s. Following stimulation, we counted hatchlings every 10 s for 1 min, then every 60 s for an additional 4 min.

Egg collection and care and playback methods follow Warkentin et al. (Warkentin et al., 2006b). We used *A. callidryas* egg clutches collected from Ocelot Pond and tested in an open-air laboratory in Gamboa. Clutches were mounted on plastic cards for support, maintained over water in plastic cups and misted several times daily to prevent desiccation. We returned all hatchlings to their pond after experiments. This research was conducted under permits from the Panamanian Autoridad Nacional del Ambiente, and approved by the Smithsonian Tropical Research Institute and by the Institutional Animal Care and Use Committee of Boston University.

Vibrations were generated by an electrodynamic minishaker (Model 4810; Bruel and Kjær, Nærum, Denmark) controlled by Canary (v. 1.2.4, Cornell Laboratory of Ornithology, Ithaca, NY, USA) on a Macintosh G4 laptop computer, *via* an external sound card (MSE-U33HB; Onkyo, Osaka, Japan) and a custom-made amplifier designed to have a flat frequency response from DC to 5 kHz (E. Hazen, Boston University Electronic Design Facility). Vibrations were transferred to the eggs *via* a minishaker-clutch interface (MCI) of stainless steel tines inserted into the clutch between eggs. Eggs were vibrated vertically, and hatchlings fell into a tray of aged tapwater. Minimum initial clutch size was 20 eggs, and all clutches fit within the MCI tine field. After MCI insertion and any hatching induced by that procedure, we allowed five hatching-free minutes before the start of a playback. We used each clutch in

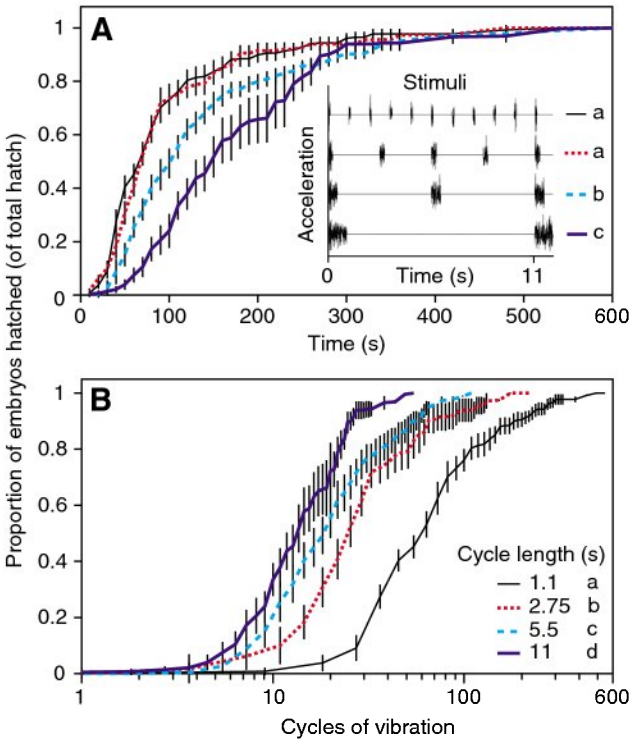

Fig. 1. Hatching response of *Agalychnis callidryas* embryos to 300 s vibration playbacks eliciting similar overall levels of hatching and matched for duty cycle but differing in cycle length. (A) Hatching as a function of time; hatching was slower with longer cycles. Inset: stimuli used in playbacks, constructed from bursts of 0–100 Hz synthetic white noise. Waveforms of 12 s of the pattern of (top to bottom) 0.1:1 s, 0.25:2.5 s, 0.5:5 s, 1:10 s duration: interval times. (B) Hatching as a function of cycles of vibration. As cycle length increased, embryos sampled progressively fewer cycles before hatching. Data are means ± s.e.m. of 10 clutches per stimulus. Different letters indicate significantly different cumulative hatching curves.

only one trial, and if ⩾25% of a clutch hatched during set-up we did not use it. To limit variation in hatching response due to egg development and diel cycle, all playbacks were conducted from 20:30–05:30 h using clutches that were 5 days old at the start of the playback session, i.e. laid six nights before the playback night. Development is highly synchronous within and among clutches laid at the same time and developing together at a site (Warkentin, 1995; Warkentin, 1999b).

Analysis of hatching response to playbacks

The total proportion of embryos hatched was not significantly different across the four stimuli (Kruskal-Wallis test: H_3=0.672, P=0.88; mean ± s.e.m., proportions hatched were 0.48±0.09, 0.49±0.07, 0.48±0.07 and 0.40±0.08 for 1.1 through 11 s cycles, respectively). Because we were interested in the timing of hatching, not the proportion hatched, we restricted subsequent analysis to only embryos that hatched during the experiments. We used two Cox regression models to test for an effect of cycle length on the amount of time and the number of cycles prior to each embryo hatching using the PHREG procedure in SAS v. 8.00 (Allison, 1995; SAS Institute, 1999). We included clutch in the model, as siblings in an egg mass are not independent. However, the survival analysis did not allow nesting clutch within cycle length. This is conservative with respect to the test for a cycle length effect, as some of its variance may be attributed to clutch. We also compared two points of interest in the hatching response using Kruskal-Wallis tests. (1) We compared latency from the start of the vibration playback until the first embryo hatched from each clutch as a measure of the minimum stimulus time, and cycles of vibration, necessary to elicit hatching. This is the value most directly comparable to hatching latency in snake attacks. (2) We compared the point of peak or modal hatching (i.e. maximum hatching rate) as a central estimate of the requirements to elicit hatching. The hatching peak is near the point at which 50% of embryos that would hatch had hatched, and 25–55 s before the mean hatching time. Mean hatching time may, however, be overestimated because we counted hatchlings only every 60 s in the last 4 min.

Hatching latency in snake attacks

As part of another study (K.M.W. and A.T.D., manuscript in preparation), we videotaped 22 attacks on 5-day-old *A. callidryas* egg clutches by two species of snakes (11 attacks per species, by five individual *Leptophis ahaetulla* L. and six individual *Leptodeira annulata* L.). Snakes were collected from ponds near Gamboa, housed in an ambient temperature and humidity laboratory in Gamboa (Warkentin, 2005) and offered egg clutches hung over trays of water in their home cages. Videotapes were recorded under infrared illumination with Digital 8 cameras (DCR-TRV120 and TRV350; Sony, Tokyo, Japan). For each attack we used the time code recorded on the videotape to measure latency of embryos to begin hatching. We considered tongue, snout or mouth contact of the snake with the clutch that was followed by biting to be part of an attack and assessed latency as the time from the first such contact until the first tadpole hatched. For 19 attacks (nine by *L. annulata*, 10 by *L. ahaetulla*) we recorded the duration from first contact until all embryos had hatched or been eaten. In three attacks the snake stopped feeding while a few eggs remained on the clutch, unhatched; we do not include these attack durations. We also calculated escape hatching success of 5-day-old clutches in 11 *L. ahaetulla* and 15 *L. annulata* attacks as the proportion of attacked embryos that were found as tadpoles in the water after the attack; not all of these attacks were videotaped. Other data on snake behavior will be reported elsewhere (K.M.W. and A.T.D., manuscript in preparation).

Results

In vibration playback experiments, both the time course of hatching and the number of cycles of the vibrational pattern sampled before hatching varied with cycle length. Hatching began earlier, peaked sooner and then tapered off in response to short-cycle stimuli, whereas it was more gradual and sustained

for longer-cycle stimuli (Fig. 1A) (Cox regression: effect of cycle length on hatching timing, χ^2=49.38, P<0.0001; clutch effect, χ^2=4.36, P=0.037). Considering hatching as a function of cycles of vibration, there was an even stronger effect of cycle length (Fig. 1B) (cycle length, χ^2=344.9, P<0.0001; clutch, χ^2=3.66, P=0.056). Embryos sampled fewer cycles of long-cycle stimuli before hatching, and the entire hatching curve was shifted to occur over progressively more cycles as those cycles became shorter. The minimum requirements for induced hatching in playbacks, measured by hatching latency as in attacks, varied with cycle length. Embryos sampled more time (vibrational stimulation) but fewer cycles (information) as cycles increased in length (Fig. 2A) (Kruskal-Wallis tests: time, H_3=8.473, P=0.037; cycles, H_3=17.604, P=0.0005). Similarly, the modal hatching point varied; embryos sampled 240% more time but 76% fewer cycles as cycles increased an order of magnitude in length (Fig. 2B) (time, H_3=19.442, P=0.0002; cycles, H_3=26.640, P=0.0001).

In snake attacks, latency until the first embryo hatched was 16±3 s (N=22 clutches, range 0.17–67 s) and did not differ between attacks by parrot snakes, *Leptophis ahaetulla*, and cat-eyed snakes, *Leptodeira annulata* (Mann–Whitney test: U=45, P=0.31). Some embryos waited longer to hatch, as snakes continued to feed, so that all eggs were not gone from the clutch until 4.8±0.8 min (N=19, range 1.3–16 min, NS between snake species; U=28, P=0.17). Escape hatching success was nonetheless high (78±2%, N=26, range 57–100%, NS between species; U=74, P=0.66).

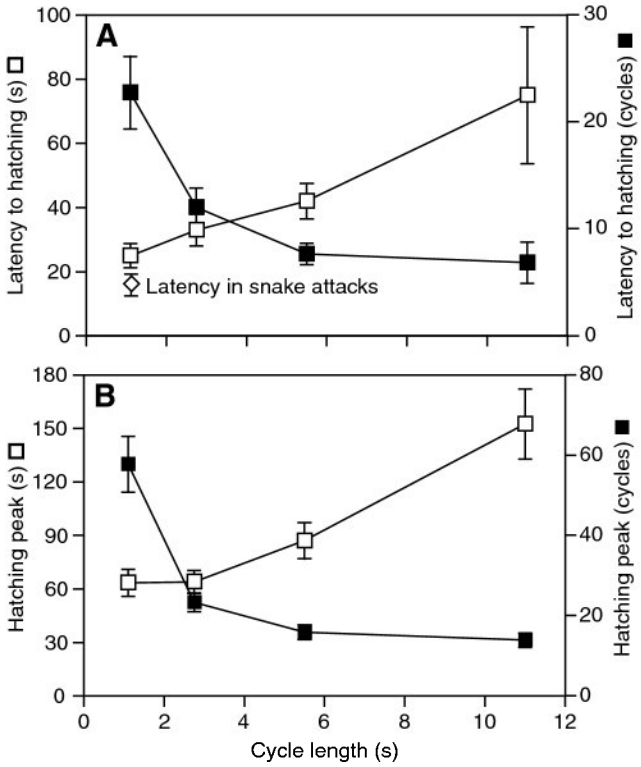

Fig. 2. (A) Latency to begin hatching and (B) peak of hatching response of *Agalychnis callidryas* egg clutches in response to vibration playbacks differing in cycle length, plotted in terms of time (open symbols) and of cycles of vibration (closed symbols). All stimuli had a 1:10 ratio of vibration to silence, and were constructed from bursts of 0–100 Hz white noise. Data are means ± s.e.m. of 10 clutches per stimulus. For comparison, latency (s) to begin hatching in snake attacks is also plotted (N=22 attacks).

Discussion

Red-eyed treefrog embryos hatch prematurely to escape from egg-eating snakes, and this escape behavior is cued by vibrations (Warkentin, 1995; Warkentin, 2005). The vibrations are caused by the snake directly moving eggs, mostly by biting them; thus they indicate imminent high risk of being eaten. Despite this, embryos rarely hatch instantly in snake attacks. On average hatching began at 16 s, and in one videotaped clutch, embryos waited over a minute before beginning to hatch. Some waited longer, as snakes continued to feed, so that all eggs were not gone from the clutch until, on average, almost 5 min after the snake began its attack. The hatching response of *A. callidryas* to synthetic vibrational stimuli was similarly measured, with many embryos taking minutes to hatch. Moreover, both the time course of hatching and the number of vibrational cycles sampled before hatching varied with cycle length, revealing that the embryos employ a flexible strategy when sampling vibrations to assess risk.

Why do attacked embryos not hatch immediately?

Attacked embryos clearly do not hatch as rapidly as they are able. Embryos hatch by performing specific movements and exit the egg in under a second (K.M.W. and M.S.C., personal observation); in two of our videotaped attacks, the first embryo hatched in 0.17 and 0.97 s. In both attacks and vibration playback trials, embryos remained basically inactive until just before hatching, then rapidly pushed out of their capsules. Thus, they experienced many seconds to minutes of stimulation before initiating hatching behavior.

In attacked clutches, the risk is highest and stimulation may be most intense close to the predator, but the risk is somewhat less immediate and stimulation may be weaker at the far side of the clutch. This might contribute to the distribution of hatching times in attacks, with embryos hatching only as the predator approaches them closely. Spatial heterogeneity in risk and/or cues cannot, however, explain the delay before the first egg – potentially the egg receiving the strongest or clearest cues – hatches. Furthermore, our vibration playback apparatus was designed to deliver vibrations uniformly across the clutch. Thus, the latency to hatch and distribution of hatching times in playback trials reflects behavioral decisions of embryos under spatially homogeneous stimulus conditions.

We suggest that the relatively long delay before attacked *A. callidryas* initiate hatching represents a period of information sampling. This is consistent with strong selection against both false alarms and missed cues (Warkentin, 1995; Warkentin, 1999a; Warkentin, 2000), which puts a premium on correct decisions. It is also consistent with both the cue properties that

red-eyed treefrog embryos use to assess risk and the variation in vibrations caused by their predators (Warkentin, 2005). Frequencies, particularly high frequencies, can be assessed rapidly, but larger-scale temporal properties, such as the duration and spacing of vibrations used by *A. callidryas* (Warkentin et al., 2006b), require more time to assess. Moreover, the variation in temporal properties of vibrations in attacks and their overlap with those in rain storms mean that information about multiple duration and interval values is required for good discrimination (Warkentin, 2005). Long sampling times may be an inevitable cost of reasonable accuracy with such cues.

The vibration sampling strategy of A. callidryas embryos

As with absolute hatching time, the variation in hatching timing across stimuli is not consistent with embryos simply hatching as fast as possible after some minimum required stimulation. Stimuli were matched for frequency, amplitude and total energy to provide a consistent amount of stimulation. They were also matched for duty cycle (ratio of vibration duration to cycle length) and the longest cycle length was shorter than the shortest mean latency to hatching (11 *vs* 25±4 s). Thus, differences in hatching timing do not reflect differential buildup of stimulation within cycles. Finally, all stimuli elicited similar levels of hatching and hatching peaked well before playbacks ended. Thus, the variation in embryo behavior is not due to differences in either the amount of simulation provided or the overall salience of the stimuli.

The variation in hatching timing is consistent with a sampling period adjusted to balance the value and cost of information (Fig. 3). In predator attacks, the largest cost of information is the risk of being killed, which increases with the pre-defense delay. For *A. callidryas*, although risk accrues at different rates in attacks by different types of predators [e.g. snakes and wasps (Warkentin et al., 2006a)], the substantial overlap in temporal properties of vibrations across predator types (M.S.C., J.G.M. and K.M.W., unpublished) makes it reasonable to consider risk simply a function of time, independent of cycle length. The value of the information is the extent to which it reduces two potentially lethal errors: missed cues that allow predators to consume eggs, and false alarms that expose vulnerable premature hatchlings to aquatic predators (Warkentin, 1995). *Agalychnis callidryas* use vibration duration and spacing to inform their hatching decision (Warkentin et al., 2006b). Information from these temporal properties is expected to accrue with cycles of vibration in some diminishing function, such that each cycle of the same pattern carries a smaller increment of information. Under such circumstances, information sampling prior to hatching should decline with increasing cycle length, as each increment of information entails more risk in longer cycles, but not to the point where sampling time remains constant. At some point, embryos should pay higher costs in order to get sufficient information (Fig. 3). The hatching behavior of *A. callidryas* appears consistent with such a model.

Studying egg behavior

Because we wanted to compare hatching timing across stimuli that vary in cycle length but elicit similar levels of hatching, we could not use the stimuli that induced the most hatching in our temporal pattern study, over 70% in a 5 min playback (Warkentin et al., 2006b). That response was close to the escape success in snake attacks, and other vibration playbacks elicit near 100% hatching (M.S.C., J.G.M. and K.M.W., unpublished). Despite the lower hatching response here, latency is not much longer with our shortest-cycle stimulus than in snake attacks (25±4 *vs* 16±3 s), and latencies for all but the longest-cycle stimulus are within the range found in snake attacks. Indeed, because we recorded hatching only every 10 s in our playback trials, we slightly overestimate hatching latency. Moreover, with all but our longest-cycle stimulus, the cumulative hatching curve leveled off within the 5 min playback period (Fig. 1). This is comparable to the hatching pattern under snake predation; attacks lasted about 5 min before all eggs had hatched or been eaten. These similarities suggest that vibration playbacks are a reasonable abstraction of the snake–egg predator–prey interaction with which to explore the behavioral decisions and information processing abilities of embryos.

Red-eyed treefrog embryos adjust their hatching timing to balance a trade-off between egg- and larval-stage risks, and

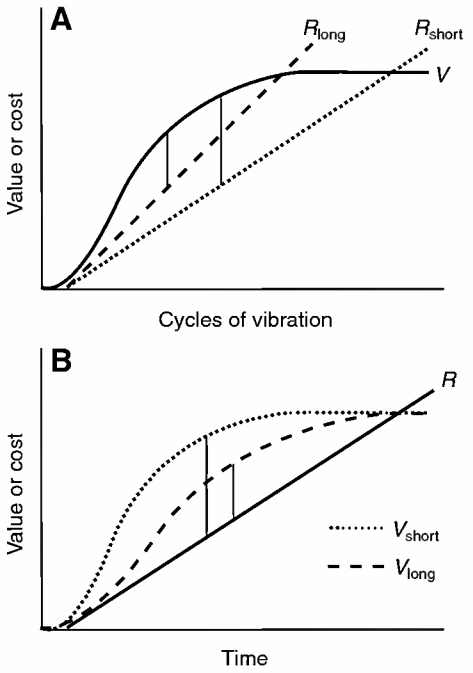

Fig. 3. A graphical model showing the hypothesized structure of the trade-off between the value of information and its cost for red-eyed treefrog eggs. Information has value (V) to the extent that it reduces potentially fatal errors about when to hatch and, for temporal properties, accrues as a diminishing function of cycles of the pattern (solid line in A). The cost of information accrues as risk of predation (R) over time (solid line in B). Elapsed time is a product of number of cycles and cycle length, thus information is more costly (A) or accrues more slowly (B) with long *vs* short cycles (subscripts). If embryos maximize net benefit (value minus cost) they should sample more time but fewer cycles if those cycles are long rather than short.

similarly context-dependent hatching timing has been shown in other taxa (Sih and Moore, 1993; Chivers et al., 2001; Li, 2002; Wedekind, 2002; Kusch and Chivers, 2004; Moreira and Barata, 2005). Here we show that *A. callidryas* embryos also modulate the amount of information on which their hatching decision is based depending on the amount of time, or risk, entailed in gathering that information. This demonstrates a second level of environmental sensitivity in the embryos' behavioral repertoire. This may be ecologically important, given the multiple risks and high levels of mortality faced by early life stages, and suggests that embryo behavior may be more complex than previously recognized.

Studying risk assessment by prey

To assess risk, prey must distinguish salient cues from noise, in any sensory modality. Elucidating the information they use, and the decision rules they apply to it, is a fundamental problem in animal behavior. Because sounds can be readily recorded, manipulated and played back to animals, bioacoustics has made great contributions to our understanding of animal behavior (Bradbury and Vehrencamp, 1998). Hunting predators, however, are often silent. Nonetheless, if they move, they produce vibrations, and there is growing evidence that these vibrations carry information to prey. Vibrations are amenable to recording, manipulation and playback techniques similar to those in bioacoustics. These techniques facilitate experiments that allow signal detection theory and information theory to be applied to studies of risk assessment. Vibration-cued antipredator responses offer an excellent opportunity to explore the information processing and behavioral decision rules that animals use in defense.

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