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The influence of predator threat on the timing of a life-history switch point: predator-induced hatching in the southern leopard frog (Rana sphenocephala)

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The influence of predator threat on the timing of a life-history switch point: predator-induced hatching in the southern leopard frog (*Rana sphenocephala*)

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Abstract: We tested the hypotheses that potential egg predators, crayfish *Procambarus nigrocinctus* and dytiscid *Cybister* sp. larvae, would accelerate the timing of hatching and that a larval predator, dragonfly naiad *Anax junius*, would delay hatching in the southern leopard frog (*Rana sphenocephala*). We also tested the hypothesis that differences in response would be proportional to predator lethality. Our results indicate that our hypotheses were partially supported. The presence of an efficient egg predator (crayfish) induces hatching faster than a less efficient predator (dytiscid larvae). However, the presence of a larval predator (naiads) did not delay hatching. Eggs that developed in the presence of egg predators produced hatchlings that were shorter (total length) than those reared in the presence of larval predators or those reared in the absence of predators. We suggest that earlier hatching times should decrease vulnerability to egg predators but result in shorter hatchlings.

Résumé : Nous avons éprouvé les hypothèses selon lesquelles des prédateurs potentiels des oeufs, l'écrevisse *Procambarus nigrocinctus* et la larve de dytique *Cybister* sp., font anticiper le moment de l'éclosion chez la grenouille léopard du sud (*Rana sphenocephala*), et un prédateur des larves, la larve de la libellule *Anax junius,* retarde l'éclosion. Nous avons aussi vérifié l'hypothèse qui veut que les différences de réaction varient en proportion du caractère létal du prédateur. Nos résultats appuient en partie ces hypothèses. La présence d'un prédateur efficace (écrevisse) suscite l'éclosion plus rapidement que celle d'un prédateur moins efficace (larve de dytique). Cependant, la présence d'un prédateur des larves (larve de libellule) ne retarde pas l'éclosion. Les oeufs qui se développent en présence de prédateurs des oeufs produisent des larves néonates plus courtes (en longueur totale) que ceux élevés en présence de prédateurs des larves ou en l'absence de prédateurs. Nous croyons que les éclosions devancées réduisent la vulnérabilité aux prédateurs des oeufs, mais elles entraînent la production de larves néonates plus courtes.

[Traduit par la Rédaction]

Introduction

Organisms occupying environments with a variable, but predictable, predator composition often develop alternative phenotypes that increase survival (Tollrian and Harvell 1999). In amphibians, these responses may take the form of changes in morphology (McCollum and Van Buskirk 1996; Van Buskirk and Schmidt 2000), behavior (Skelly 1997), or timing of life-history switch points, such as metamorphosis (Wilbur and Fauth 1990) and hatching (Sih and Moore 1993; Warkentin 1995).

Antipredator responses often reduce time available for other activities, such as feeding and reproduction (reviewed by Lima and Dill 1990). Also, it has been demonstrated that predators may differ in their ability to capture and consume prey (e.g., Kiesecker et al. 1996; Relyea 2001*a*). Therefore, if prey respond to all predators equally, unnecessary reductions in growth and fecundity may be incurred. Thus, it is thought to be beneficial for prey to evaluate predator threat and respond accordingly (Sih 1987; Lima and Dill 1990; Lima 1998). Anuran larvae can distinguish between different predators (Relyea 2001*a*, 2001*b*; Van Buskirk 2001), as well as nonpredators (Kiesecker et al. 1996). However, the hypothesized adjustment of antipredator responses to threat from multiple species of predator has not been supported (Relyea 2001*a*).

Since the seminal work of Wilbur and Collins (1973), amphibians have been commonly used in the study of life-history changes. Factors such as metamorph size and timing of life-history switch points are influenced by pond permanence (Newman 1988) and predation (Wilbur and Fauth 1990; Warkentin 1995; Sih and Moore 1993). After a life-history change, the suite of potential predators may change significantly (Werner and Gilliam 1984). Theoretical (Werner 1986) as well as empirical studies (Sih and Moore

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1993; Warkentin 1995) suggest that amphibians take advantage of these changes and adjust the timing of life-history switch points to reduce predation. For example, some anurans shorten the embryonic stage (accelerate hatching) as a response to egg predators (Warkentin 1995; Chivers et al. 2001; Saenz et al. 2003). Conversely, in the salamander *Ambystoma barbouri*, presence of larval predators increases the duration of the embryonic stage, delaying hatching (Sih and Moore 1993; Moore et al. 1996). Changes in the timing of hatching due to the presence of predators may result in morphological differences among hatchlings that may in turn affect survivorship in the next (larval) life stage (Sih and Moore 1993; Moore et al. 1996; Warkentin 1999*a*, 1999*b*).

The focus of this study was to experimentally determine the effects of different predators on the timing of hatching in the southern leopard frog (*Rana sphenocephala*). Our hypotheses were (*i*) different predator species pose different threats to *R. sphenocephala* eggs, (*ii*) predators that readily consume eggs will accelerate hatching, while predators that pose the greatest threat during the larval life stage will delay hatching, (*iii*) the timing of hatching should be relative to predator threat, where voracious egg predators accelerate hatching more than egg predators that pose a moderate threat, (*iv*) differential timing of hatching may result in differences in hatchling morphology (i.e., early hatching may result in shorter hatchlings and delayed hatching may result in longer hatchlings).

Materials and methods

Predators

This study used common predators that coexist with *R. sphenocephala* eggs and larvae in eastern Texas. These included the crayfish *Procambarus nigrocinctus*, the dytiscid *Cybister* sp. larvae, and the dragonfly naiad *Anax junius*. Crayfish have been cited as a larval and egg predator on amphibians (Figiel and Semlitsch 1991) and are a significant threat to *R. sphenocephala* eggs (Saenz et al. 2003). Dytiscid larvae are active foragers (J.B.J., D.S., and C.K.A., personal observation); thus, they may potentially prey on eggs. Finally, *A. junius* naiads have been shown to inflict considerable mortality on anuran larvae (Brockelman 1969; Van Buskirk 1988). Generally, prey movement is required to elicit an attack response (Folsom and Collins 1984). Therefore, predation on eggs by naiads seems unlikely, based on their foraging strategy; however, this remains to be tested.

We collected *R. sphenocephala* egg masses (N = 20), dytiscid larvae (N = 20, 40–55 mm total length), naiads (N = 20, 35–45 mm total length), and crayfish (N = 20, 75–90 mm total length) from the Stephen F. Austin Experimental Forest and the Davy Crocket National Forest on 20–21 January 2002. The eggs were at approximately stage 4–5 (Gosner 1960). Our experimental trials began immediately after eggs were obtained. All animals used in this study were cared for in accordance with the guidelines of the Canadian Council on Animal Care.

Predator threat experiment

We added approximately 2 L of aged tap water and one of three predators (crayfish, dytiscid larva, or naiad) to three 3-L plastic tubs (19 cm × 9 cm × 33.5 cm). Predators were not fed 24 h prior to the start of this experiment. We then placed 10 eggs from a single *R. sphenocephala* egg mass (full siblings) in each tub with their respective predator. These three tubs constituted a block, which was replicated with 20 different egg masses (assumed to be unrelated). After 24 h, we counted the number of eggs eaten by each predator and the number of predators that ate eggs. Data were arcsine square-root transformed and the mean of each treatment was calculated. Treatment means were subjected to an unpaired Student's t test to compare the threat posed by the respective egg predators (crayfish and dytiscid larvae). Data on the number of egg predators eating in each treatment were compared using Fisher's exact test.

Predator effects on hatching experiment

We added 2 L of aged tap water and a plastic cage (14 cm × 9 cm × 14 cm), which was covered with fiberglass screening to allow water flow, to six 3-L plastic tubs (19 cm × 9 cm × 33.5 cm). Each cage received one of the following five predator treatments: unfed crayfish, fed dytiscid larva, unfed dytiscid larva, fed naiad, unfed naiad. The sixth cage remained empty, which represented our control. We removed six 20-egg clumps from each egg mass and assigned each to a different tub. Therefore, we blocked by egg mass so that each replicate contained full-sibling eggs. Our experiment contained 20 replicates (egg masses assumed to be unrelated). Predators in the fed predator treatments were fed one *R. sphenocephala* larva once daily. We monitored each tub once an hour. We defined hatching as the point at which one half the hatchlings had left the jelly (Laurila et al. 2001). Once one half of the hatchlings had left the jelly, we pulled the tub from the experiment and preserved the hatchlings and the remainder of the egg mass in 10% formalin. Crayfish are known to induce hatching in *R. sphenocephala* eggs even if not fed (Saenz et al. 2003); therefore, we did not have a fed crayfish treatment in this study. Five blocks were removed from this experiment because of a pathogenic infection (water mold or fungus). The number of hours to hatching for each tub was recorded and treatments were compared using a randomized block ANOVA followed by Tukey's studentized range test.

Hatchling morphology

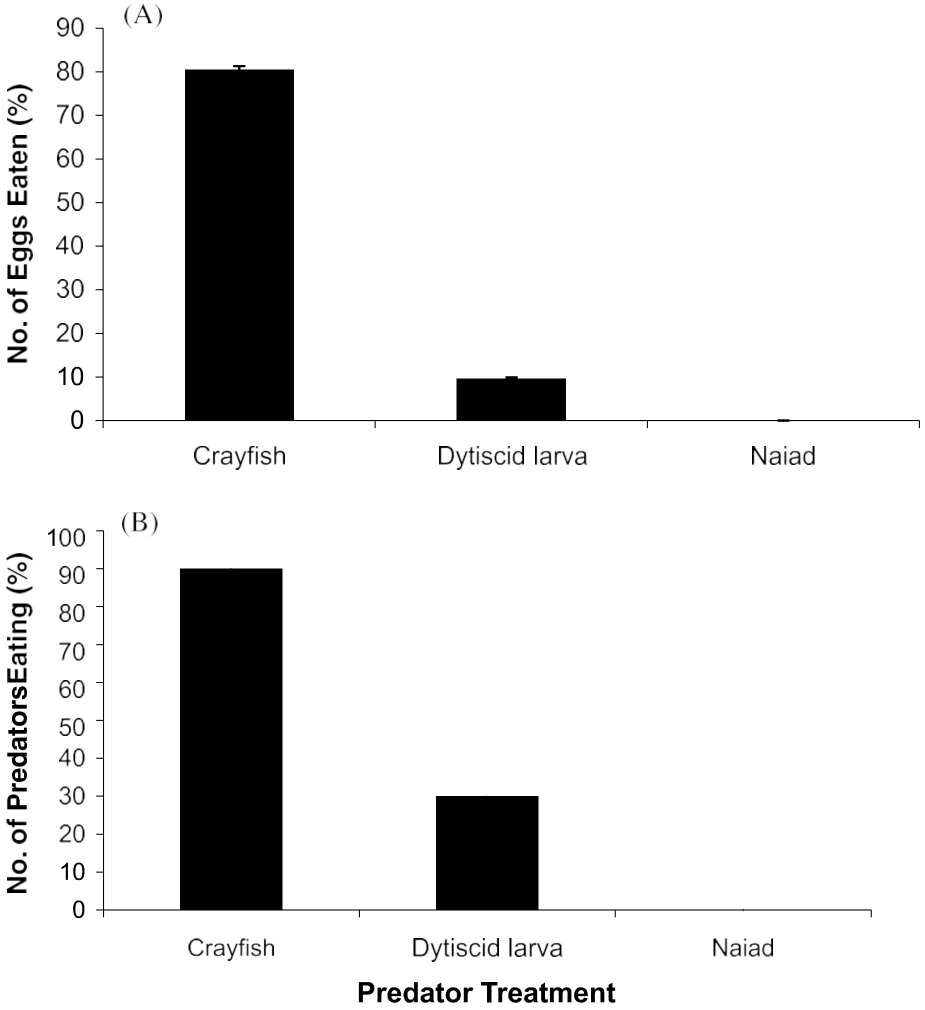
Each hatchling was measured with calipers under a dissection scope. Because of the small size of the hatchlings (4.5–7 mm), we only measured total length. We were unable to determine hatchling developmental stage (Gosner 1960) because a number of the characters used to determine development stage were unavailable post mortem. The mean value of total length for each tub was calculated and treatments were compared using a randomized block ANOVA with Tukey's studentized range test.

Results

Predator threat to eggs

Naiads did not eat *R. sphenocephala* eggs in our experiment (Fig. 1). Egg consumption by crayfish and dytiscid larvae differed significantly (t = 7.46, $P \leq 0.001$). Crayfish proved to be the greatest threat to *R. sphenocephala* eggs in

Fig. 1. Results of the experiment to determine the relative consumption patterns of predators (crayfish *Procambarus nigrocinctus*, dytiscid *Cybister* sp. larvae, and naiad *Anax junius*, respectively) on *Rana sphenocephala* eggs. (A) Percentage of *R. sphenocephala* eggs eaten by crayfish, dytiscid larvae, and naiads. (B) Percentage of crayfish, dytiscid larvae, and naiads consuming *R. sphenocephala* eggs.



our experiment, consuming 80.5% of the eggs (Fig. 1A). Dytiscid larvae consumed only 9.5% of the eggs (Fig. 1A). The number of crayfish eating eggs differed significantly from that of the dytiscid larvae (Fisher's exact test, $P \leq 0.001$). A majority (90%) of the crayfish ate eggs (Fig. 1B). Only 30% of the dytiscid larvae consumed *R. sphenocephala* eggs (Fig. 1B).

Predator effects on timing of hatching

Predator treatment had a significant effect on timing of hatching ($F_{[14]} = 16.47$, $P < 0.001$). Crayfish significantly shortened the length of time to hatching compared with the other treatments (Fig. 2). Unfed dytiscid larvae significantly accelerated hatching compared with fed naiad, fed dytiscid larvae, and control treatments (Fig. 2). The naiad and fed dytiscid treatments did not differ significantly from the control treatment (Fig. 2).

Hatchling morphology

We found significant differences in the total length of *R. sphenocephala* hatchlings between predator treatments ($F_{[5]} = 8.87$, $P < 0.001$). In the presence of crayfish, hatchlings emerged significantly shorter (total length) than hatchlings in the other two treatments (Fig. 3). Hatchlings in the presence of unfed dytiscid larvae were significantly shorter than hatchlings in the control but did not differ from the fed dytiscid larvae or either naiad treatment (Fig. 3).

Discussion

As we had hypothesized, *R. sphenocephala* adjusted the timing of hatching differently in the presence of different predators. Crayfish consumed a significantly larger proportion of *R. sphenocephala* eggs than dytiscid larvae, and crayfish induced significantly faster hatching than dytiscid larvae. Similar differential responses occur in the red-eyed treefrog (*Agalychnis callidryas*) with respect to egg predation by two functionally different predators, wasps and snakes. Snakes attack the egg mass and as a result induce hatching within the entire mass. Wasps disturb the egg mass considerably less than snakes, as they predate one egg at a

Fig. 2. Results of ANOVA of mean numbers of hours to hatching in *R. sphenocephala* eggs in the crayfish, unfed dytiscid larvae, fed dytiscid larvae, unfed naiad, fed naiad, and control treatments. NS, not significant.

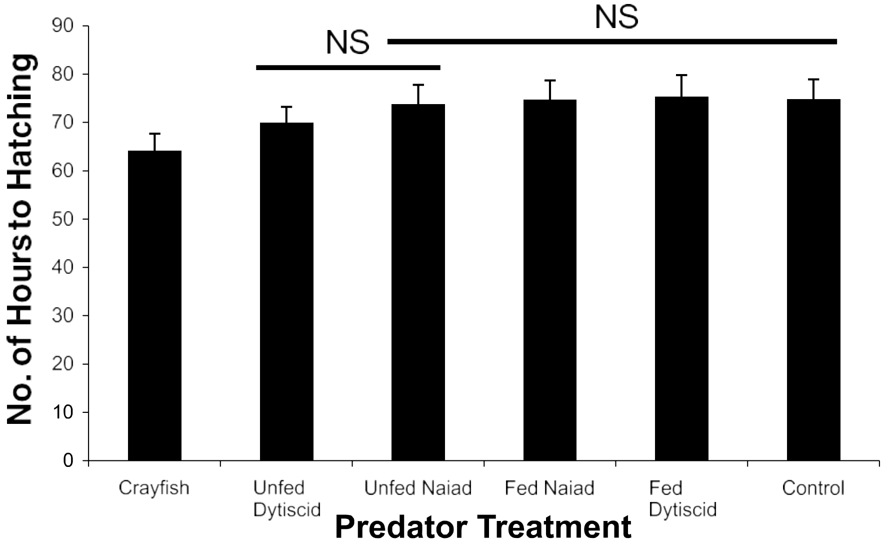
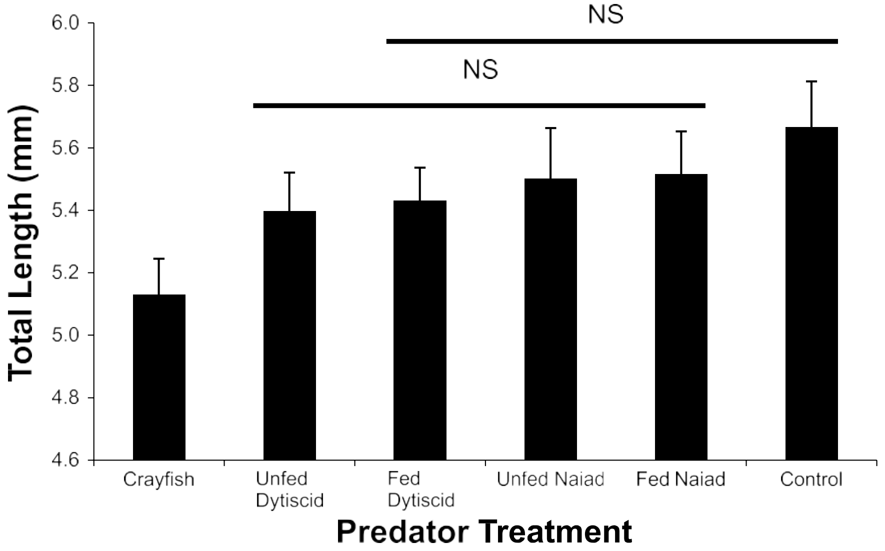


Fig. 3. Results of ANOVA of mean of total length of *R. sphenocephala* hatchlings hatched from the crayfish, unfed dytiscid larvae, fed dytiscid larvae, unfed naiad, fed naiad, and control treatments. NS, not significant.



time, which causes only individual eggs to hatch (Warkentin 2000).

Dytiscid larvae fed *R. sphenocephala* tadpoles did not affect timing of hatching, although the unfed treatment did significantly accelerate hatching (Fig. 2). Cues produced by larval conspecifics when consumed by predators may indicate that a larval predator is present (Belden et al. 2000). In such a situation, accelerated hatching may not decrease predation on eggs. Both the unfed crayfish and the unfed dytiscid larvae accelerated hatching. Potential egg predators may be labeled by default in such instances when no conspecific cues are available.

Our data suggest that naiads are not egg predators, as they did not consume any eggs in our trials (Fig. 1). We hypothesized that the presence of such a larval predator would extend the embryonic stage. We did not observe this in our experiment and suggest three possible reasons. First, naiads may not significantly prey on hatchlings. Therefore, extension of the embryonic stage may not be of any benefit against these predators. This seems feasible considering that hatchlings remain relatively immobile until the mouthparts open (J.B.J., D.S., and C.K.A., personal observation) at stage 21 (Gosner 1960) and food can be taken from the environment. Second, *R. sphenocephala* eggs may be unable to detect or respond to chemical signals that would inform them of the predator environment, essentially a phenotype–environment mismatch (Moran 1992; Getty 1996; DeWitt et al. 1998). Third, *R. sphenocephala* may use different antipredator defenses against larval predators rather than an alteration in the timing of hatching.

Changes in morphology co-occurred with the effects of predators on the timing of hatching; hatching early resulted in shorter hatchlings. Therefore, we suggest that differences in hatchling size are likely a direct consequence of hatching early.

Early hatching may have a cost. Shorter total length may indicate smaller size, and smaller size at hatching may increase predation risk (Warkentin 1995, 1999*a*, 1999*b*).

Numerous models concerning foraging and life history assume that prey can perceive the level of threat that predators pose and that antipredator responses are proportional to that threat (reviewed by Van Buskirk and Arioli 2002). Yet, this hypothesis has received little empirical attention with regard to anurans (e.g., Relyea 2001*a*; Van Buskirk and Arioli 2002). Van Buskirk and Arioli (2002) suggested that antipredator morphological features (tail depth) increase relative to elevated consumption of conspecifics from one species of predator. Relyea (2001*a*) evaluated the threat of numerous predator species and then experimentally examined several morphological and behavioral antipredator responses in a number of species of larval anurans. The author found that larval anurans respond to predators specifically, utilizing different defenses against different predators. However, evidence of increases in response relating to increasing threat was not found. If a defense is ineffective in matching predator threat, other defenses may increase to mediate this deficit, i.e., trait compensation (DeWitt et al. 1999). Unfortunately, few studies have addressed trait compensation in anurans (e.g., Brown and Taylor 1995). Future work concerning the hypothesis of antipredator response being commensurate to predator threat should examine trait compensation between multiple phenotypic characters.

In conclusion, our data suggest that *R. sphenocephala* accelerate hatching faster with more dangerous predators. Additionally, the timing of hatching in *R. sphenocephala* is influenced by predator diet. More work should involve chemical cues produced by eggs and their subsequent effect on the timing of hatching and hatchling morphology.

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