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Terrestrial predators and abiotic conditions affect hatching survival of arboreal frog eggs: Implications for aquatic food web dynamics

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Introduction
Organisms with complex life cycles (e.g., amphibians, aquatic insects) that use both habitats sequentially through development are important links between aquatic and terrestrial food webs. The flux of these organisms moving between habitats can have important consequences for food web dynamics in adjacent ecosystems. Anuran species with arboreal eggs are vulnerable to a suite of abiotic threats and terrestrial predators. The larval (tadpole) stage of these species are important herbivores. Therefore, the degree to which terrestrial predators or abiotic conditions reduce the input of tadpoles into the aquatic environment may carry important indirect consequences for aquatic ecosystem dynamics (e.g., tadpole herbivory).

Hypothesis 1: Terrestrial predators and abiotic conditions influence the density of their herbivorous tadpole prey.

Hypothesis 2: Changes in the density of tadpoles alters feeding rates and nutrient inputs, which affect aquatic ecosystem processes

Methods
- Field Monitoring: We monitored clutch density, survivorship and sources of mortality throughout the breeding season. We monitored a subset of new clutches 2x/d through to hatching.
- Mesocosm Experiments: Using parameters from field monitoring we investigated how tadpole density affects aquatic primary productivity via consumption and through potential competition with zooplankton (8 initial densities each replicated 2x).

Results
- We monitored 201 clutches and ~ 7,335 developing embryos (mean clutch size 36.17 eggs clutch$^{-1}$ (mean ± SD)).
- Overall, 49% of all eggs laid survived to the tadpole stage.

Figure 1. Clutch density varied over the course of the season and among ponds (GLM, month, $F_{max} = 5.69, P = 0.4,\quad$ pond $F_{max} = 7.36, P = 0.044$).

Figure 2. Major sources of mortality for clutches over the entire season and across both ponds.

Figure 3. Different sources of mortality resulted in differences in clutch survival (GLM, fate, $F_{max} = 8.05, P = 0.0006$).

Figure 4. Ambient hatching inputs for Ocelot pond compared to estimated reductions due to predators and abiotic conditions.

Figure 5. Initial tadpole density had a significant negative effect on final zooplankton density (Table 1).

Figure 6a. Exploring phytoplankton growth over time as a function of tadpole density.

Figure 6b. Density dependent tadpole growth. Initial tadpole density had a significant negative effect on final tadpole biomass.

Table 1. Model selection (sucrose feeding rates as an overall parameter for examining the effect of tadpole density on phytoplankton growth).

<table>
<thead>
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<th>Model</th>
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<td>0</td>
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<tr>
<td>Linear</td>
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<td>154</td>
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Asymptotic values as an overall parameter for examining the effect of tadpole density on phytoplankton growth

Figure 7, the negative exponential has the maximum likelihood estimates. E.g., For Figure 6a, density mediated effects may help explain the trait mediated effects of tadpoles on phytoplankton (these embryos exhibit early hatching in response to predators).

Take Home and Future Directions
Taken together our results show that the interpretations of food web dynamics can be quite different depending on the suit of focal species. For example at low tadpole densities we might assume that the reduction in tadpole inputs due to predator and abiotic factors would have a positive effect on primary productivity (Fig. 6a). However, at these low densities, zooplankton density decreases which will have a negative effect on primary productivity. Theory predicts that our patterns could result from either population level effects (e.g., intraspecific competition) or from community effects (e.g., interspecific competition with zooplankton, Fig 7). Future analyses will begin to explore the underlying mechanisms driving these patterns.

Other questions will we continue to explore include:
- Why would resources continue to decrease even though overall consumer biomass is drastically reduced (Fig. 5)?
- Data (not shown here) also suggest that density mediated effects may help explain the trait mediated effects of tadpoles on phytoplankton (these embryos exhibit early hatching in response to predators).

Given the variation in tadpole inputs due to breeding phenology, abiotic conditions and predators highlight the dynamical effects of any underlying mechanisms predicted by classical ecology may be context dependent.

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