

Effects of beaver on the thermal biology of an amphibian

David K. Skelly¹ and L. Kealoha Freidenburg²

¹School of Forestry & Environmental Studies, Department of Ecology & Evolutionary Biology, Yale University, 370 Prospect Street, New Haven, CT 06520, U.S.A.

E-mail: david.skelly@yale.edu

²Department of Ecology & Evolutionary Biology, University of Connecticut, 75 N. Eagleville Road, Storrs, CT 06269, U.S.A.

Abstract

It is often assumed that ecological interactions happen at rapid rates relative to evolutionary change. In this study we examined the development and physiology of an amphibian (*Rana sylvatica*) from populations found in forested wetlands, and from wetlands that had been cleared by reinvading beaver (*Castor canadensis*). Embryos from beaver wetlands hatched at lower rates when raised in a shaded, common garden setting compared with embryos from forested wetlands. Larvae from beaver wetlands had higher critical thermal maxima compared with conspecifics from forested wetlands. These patterns suggest that *R. sylvatica* populations may have diverged rapidly (in less than 36 years) in response to changes in their environment induced by another species. Other agents of thermal change, such as anthropogenic landscape conversion or alteration of global climate, could have analogous impacts on wetland dependent species such as amphibians.

Ecology Letters (2000) 3: 483–486

INTRODUCTION

For much of the history of their discipline, ecologists have generated predictions of distribution and abundance while presuming that important aspects of phenotype will remain constant. In more recent years, ecologists have begun to recognize the two primary modes of phenotypic change, plasticity and evolution (e.g. Grant & Grant 1995; Fauth 1998).

The question of whether species evolve rapidly is of increasing importance as humans introduce exotics, wipe out natives, and reintroduce others all at ever increasing rates. With few exceptions (e.g. Kiesecker & Blaustein 1997; Huey *et al.* 2000), we have no knowledge of the existence or impact of such changes.

One important example is the reinvasion of the beaver (*Castor canadensis*). This species was eliminated from large regions of eastern North America beginning in the eighteenth century due to trapping and is now reinvading much of its former range (Morgan 1868; Townsend & Butler 1996). Because they alter vegetation and hydrology, it has long been postulated that beaver may have substantial impacts on other wetland dependent species (Naiman *et al.* 1986; Snodgrass & Meffe 1998; Schlosser & Kallemeyn 2000).

In this study we evaluate the hypothesis that beaver induced modifications of wetlands have led to evolution of thermal physiology and development among resident amphibians. This hypothesis is based on measurement of

the thermal environment of wetlands. Compared with heavily shaded wetlands, beaver wetlands experience water temperatures that can average 2°C warmer, with peak temperatures up to 15°C higher on cloudless days (D.K. Skelly and L.K. Freidenburg, unpublished data). We focused our experiments on the wood frog (*Rana sylvatica*). This species is well studied (e.g. Berven 1987, 1990; Skelly *et al.* 1999) and is widespread among wetlands in New England.

We conducted two experiments, focusing on *R. sylvatica* populations from forested and beaver wetlands. In the first we assessed hatching by *R. sylvatica* embryos in a common garden setting in which half of the experimental containers were exposed to full sun and the remainder were exposed to 30% of incident sunlight. In the second experiment, we assayed the critical thermal maximum of laboratory reared larvae collected from the two wetland types.

METHODS

We conducted our experiments using *R. sylvatica* collected from six wetlands at the Yale-Myers Forest (3500 ha) in north-eastern Connecticut. Three of these wetlands are known to have been invaded by beaver since 1964, while the remaining three have not (D.M. Smith, personal communication). Aerial photographs confirm that all six wetlands had dense forest canopies prior to beaver invasion (J. Foster, unpublished data). Each wetland is

known to dry on an annual basis and to range in surface area from $\approx 600 \text{ m}^2$ to approximately 5000 m^2 and in maximum depth from 48 to 150 cm. Currently, the light environment in the two wetland types differs dramatically. Owing to woody vegetation dominated by red maple (*Acer rubrum*) and eastern hemlock (*Tsuga canadensis*), the wetlands without beaver have dense canopy cover (averaging 89% vs. 10% cover for beaver wetlands).

We conducted a hatching experiment from 27 March (day 0) until 14 April (day 18) 2000. Two egg masses were collected from each of six wetlands within 24 h of oviposition (and at Gosner Stages 1 or 2; Gosner 1960) and held at 10°C . On day 0, groups of 10 eggs were surgically excised from egg masses while preserving the integrity of the jelly envelope. Single clumps were placed into plastic containers ($39 \times 25 \times 14 \text{ cm}$) holding 8 L of well water aged $> 24 \text{ h}$, and placed outdoors on a wooden platform.

Containers were subject to one of two shading treatments. Shaded containers were placed under two layers of screening (fiberglass, 1.7 mm mesh), which prevented 70% of incident light from reaching the container. Open containers were exposed to the full intensity of incident sunlight.

Shading was crossed with wetland type: beaver or forested. A population treatment was nested in wetland type treatment (three wetlands per type). Each treatment combination was replicated four times. Two additional containers held submersible temperature loggers (Onset Corp.), to record temperatures in a shaded and an open container every 30 min. Containers were regularly inspected to assess hatching condition of embryos. An individual was considered hatched when it was entirely clear of the egg envelope. We present results from an analysis of variance on the number of individuals hatched on day 18.

The critical thermal maximum (CTM) experiment was conducted on 15–17 May 2000 following standard methods (Hutchison 1961; Hoppe 1978). Larvae were derived from the same stocks used in the embryonic development experiment and were maintained in wading pools and fed an ad libitum ration of senesced leaves and rabbit chow.

Single individuals were placed in Ehrlenmayer flasks holding 200 mL of well water aged $> 24 \text{ h}$. Flasks were then placed in a recirculating, temperature controlled water bath. An additional flask placed in the centre of the bath held a thermometer used to record CTM. Groups of eight flasks were run during successive trials. A run consisted of allowing the temperature to equilibrate to 20°C and then elevating the water bath temperature by 0.5°C per min. At each 0.5°C elevation of temperature, each tadpole was prodded with a glass rod. CTM was designated as the

temperature at which tadpoles showed no righting response and were unresponsive. In practice, CTM was unmistakable. Larvae became increasingly active as temperature was elevated; the attainment of CTM involved a rapid, dramatic shift to complete inactivity.

RESULTS

In the hatching experiment, shading containers resulted in a 0.6°C drop in average temperature (8.1°C vs. 7.5°C) and a decline of up to 5.0°C in peak daytime temperature (Fig. 1). Embryos of *R. sylvatica* hatched more rapidly in open vs. shaded containers (Fig. 2; ANOVA: $F_{1,40} = 26.80$, $P < 0.001$). There was no main effect of wetland type (ANOVA: $F_{1,40} = 2.98$, $P = 0.092$). Nearly all embryos, regardless of population origin, had hatched in open containers by day 18. However, there was a significant interaction between wetland type and shading treatment (ANOVA: $F_{1,40} = 5.98$, $P = 0.019$) reflecting the effect of wetland type on hatching in shaded containers. On day 18, 46% more embryos from forested wetlands had hatched compared with embryos from beaver wetlands.

Critical thermal maximum of tadpoles from beaver wetlands was 0.4°C higher than that of tadpoles from forested wetlands (Fig. 3; ANOVA: $F_{1,36} = 8.40$, $P = 0.006$).

DISCUSSION

The activities of beaver can dramatically change wetland environments (Naiman *et al.* 1986). By felling or drowning overstory vegetation, beaver can flood formerly shaded wetlands with light. These shallow bodies of water can become significantly warmer in the process. We found that beaver are associated with decreased rates of hatching and an enhanced ability to cope with higher temperatures among populations of an amphibian, *R. sylvatica*.

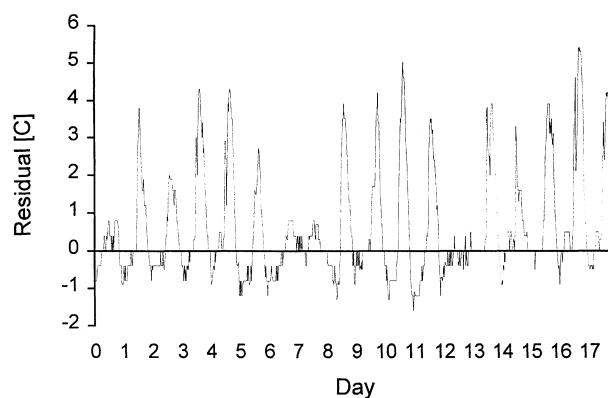


Figure 1 Effect of shading on water temperature in containers used in hatching experiment. Residual is the difference in temperature between an open and a shaded container recorded every 30 min between day 0 and day 18 of the experiment.

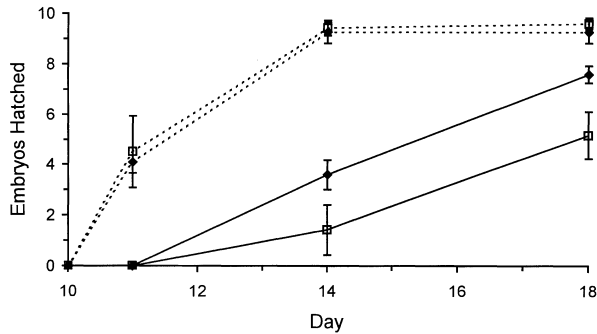


Figure 2 Time course of hatching by embryos of *R. sylvatica* exposed to full (dashed line) or 30% incident (solid line) sunlight in a common garden setting. Embryos were collected from beaver (open symbols) or forested (closed symbols) wetlands. Each point represents the average from three wetlands of each type. Error bars represent 1 SE. No hatching occurred prior to day 10 of the experiment.

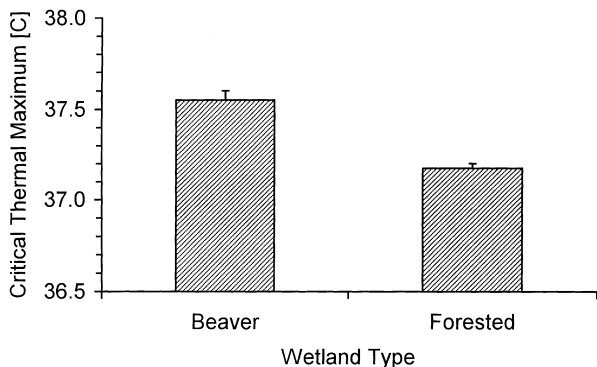


Figure 3 Critical thermal maxima for *R. sylvatica* larvae (≈ 54 mg body weight) from two wetland types, beaver and forested. For each wetland type, responses from two wetlands have been averaged. Ten larvae were assessed from each wetland. Error bars represent 1 SE.

The patterns we uncovered could reflect (1) maternal effects, (2) the presence of previously unrecognized clades, or (3) the effects of local adaptation (Futuyma 1998). Maternal effects seem unlikely in the absence of differences in embryo size or stage at the onset of the experiment and because embryos were brought to the laboratory environment soon after laying.

Further research will be required to unambiguously distinguish between the existence of type specific clades vs. localized adaptation. In either case, there is evidence of an evolved match between habitat use and phenotype. The distinction between explanations is one of rate. In the first case, the landscape changes rapidly relative to phenotype. If this is so, our results suggest that populations are capable of choosing oviposition sites based on pertinent cues (Resetarits & Wilbur 1989; Blaustein 1999), and can reshuffle rapidly via dispersal

(Berven & Grudzien 1990) to new wetlands in order to keep pace with environmental change.

In the second case, phenotype changes rapidly relative to landscape. At Yale-Myers Forest, this would mean divergence of phenotypes within 36 years of beaver reinvasion. While this is certainly rapid given the lifespan of *R. sylvatica* (≤ 4 years, Berven 1990), it is not outside the boundaries of previous observations of phenotypic evolution (Hendry & Kinnison 1999).

Regardless of the particular mechanism, the thermal biology of the *R. sylvatica* populations we studied seems to signal the effects of past selection. In cooler, forested wetlands, selection could reflect particularly strong pressure on anurans to reach metamorphosis prior to pond drying. In warmer wetlands, where development proceeds more rapidly, possible advantages of delaying hatching could include avoidance of larval predators (Warkentin 1999) or other mortality sources. The existence of higher CTM in beaver wetlands may reflect exposure to extreme water temperatures (over 40°C) not experienced in forested wetlands.

Beaver are not the only agents of landscape conversion and thermal modification. It is plausible that cutting of forests adjacent to wetlands, or global changes in climate also may lead to responses. If amphibians and other wildlife are broadly sensitive to such thermal disturbances, such responses have significant implications for ecologists and conservation professionals.

ACKNOWLEDGEMENTS

M. Urban, C. Burns, A. Halverson, T. O'Connor, O. Schmitz, and H. zu Dohna provided invaluable assistance during the experiments as well as comments on the manuscript. Thanks to J. Foster for the use of unpublished data. This research was supported by a gift from Mrs. E. S. Dwyer.

REFERENCES

- Berven, K.A. (1987). The heritable basis of variation in larval developmental patterns in the wood frog (*Rana sylvatica*). *Evolution*, 41, 1088–1097.
- Berven, K.A. (1990). Factors affecting fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology*, 71, 1599–1608.
- Berven, K.A. & Grudzien, T.A. (1990). Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. *Evolution*, 44, 2047–2056.
- Blaustein, L. (1999). Oviposition site selection in response to risk of predation: evidence from aquatic habitats and consequences for population dynamics and community structure. In: *Evolutionary Theory and Processes: Modern Perspectives, Papers in Honor of Eviator Nevo* (ed. Wasser, S.P.). Kluwer, The Netherlands, pp. 441–456.

- Fauth, J.E. (1998). Investigating geographic variation in species interactions using common garden experiments. In: *Experimental Ecology: Issues and Perspectives* (eds Resetarits, W.J. Jr & Bernardo, J.). Oxford, New York, pp. 394–415.
- Futuyma, D.J. (1998). *Evolutionary Biology*, 3rd edn. Sinauer, Sunderland, MA.
- Gosner, K.L. (1960). A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, 16, 183–190.
- Grant, P.R. & Grant, B.R. (1995). Predicting microevolutionary responses to directional selection on heritable variation. *Evolution*, 49, 241–251.
- Hendry, A.P. & Kinnison, M.T. (1999). The pace of modern life: measuring rates of phenotypic microevolution. *Evolution*, 53, 1637–1653.
- Hoppe, D.M. (1978). Thermal tolerance in tadpoles of the chorus frog *Pseudacris triseriata*. *Herpetologica*, 34, 318–321.
- Huey, R.B., Gilchrist, G.W., Carlson, M.L., Berrigan, D. & Serra, L. (2000). Rapid evolution of a geographic cline in size in an introduced fly. *Science*, 287, 308–309.
- Hutchison, V.H. (1961). Critical thermal maxima in salamanders. *Physiol. Zool.*, 34, 92–125.
- Kiesecker, J.M. & Blaustein, A.R. (1997). Population differences in responses of red-legged frogs (*Rana aurora*) to introduced bullfrogs. *Ecology*, 78, 1752–1760.
- Morgan, L.H. (1868). *The American Beaver and his Works*. Dover, New York.
- Naiman, R., Melillo, J.M. & Hobbie, J.M. (1986). Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology*, 67, 1254–1269.
- Resetarits, W.J. Jr & Wilbur, H.M. (1989). Oviposition site choice by *Hyla chrysoscelis*: role of predators and competitors. *Ecology*, 70, 220–228.
- Schlosser, I.J. & Kallemeyn, L.W. (2000). Spatial variation in fish assemblages across a beaver-influenced successional landscape. *Ecology*, 81, 1371–1382.
- Skelly, D.K., Werner, E.E. & Cortwright, S.C. (1999). Long-term distributional dynamics of a Michigan amphibian assemblage. *Ecology*, 80, 2326–2337.
- Snodgrass, J.W. & Meffe, G.K. (1998). Influence of beavers on stream fish assemblages: effects of pond age and watershed position. *Ecology*, 79, 928–942.
- Townsend, P.A. & Butler, D.R. (1996). Patterns of landscape use by beaver on the lower Roanoke River floodplain, North Carolina. *Phys. Geogr.*, 17, 253–269.
- Warkentin, K.M. (1999). Effects of hatching age on development and hatchling morphology in the red-eyed treefrog, *Agalychnis callidryas*. *Biol. J. Linnean Soc.*, 68, 443–470.

BIOSKETCH

David Skelly is an ecologist interested in large scale, long-term distributional patterns. His primary research has centred on the ecology and behaviour of amphibians inhabiting temporary ponds.

Editor, L. Blaustein

Manuscript received 1 August 2000

First decision made 30 August 2000

Manuscript accepted 13 September 2000