**Life history dynamics of the tiger salamander, *Ambystoma tigrinum*, in response to Pleistocene climate**

Amphibians are sensitive proxies for environmental change. As ectodermic vertebrates, they are directly affected by the temperature of the external environment. In addition, their complex life cycle exposes them to both aquatic and terrestrial environments, with different humidity and moisture conditions, as well as distinct biotas comprised of food, competitors, and predators. Recent studies have shown that amphibian populations are declining worldwide due to habitat degradation as a result of climate change and disease (Collins and Storfer 2003, McMenamin and Hadly 2010, Reading 2007, Stuart 2004). In particular, McMenamin and Hadly (2010) discovered that increasing temperature and decreasing rates of precipitation in the world's first national park, Yellowstone National Park, have led to the disappearance of pond habitats of the local tiger salamander population (*Ambystoma tigrinum*), and a dramatic loss to its population abundance and distribution (McMenamin et al. 2008). This environmental stress is manifest in changes in life history traits such as body size, developmental timing, and feeding habits, all of which potentially threaten the survival of the populations in the region.

In order to preserve amphibians, we must first understand their responses to regional and global environmental changes at the individual and population levels. This kind of knowledge can be acquired through paleontological studies of past amphibian populations and how they have responded to climatic fluctuations, and is of key interest to conservation biology.

I will investigate the impact of Pleistocene environments on the population-level dynamics and life history of the tiger salamander (*Ambystoma tigrinum*), the most widely distributed salamander in North America, by analyzing a  Pleistocene [100 to 40 thousand years (ka)] fossil record that was recently excavated at the Snowmastodon field site in Snowmass Village, Colorado. Furthermore, I will access the present threat facing *Ambystoma* populations by comparing the population-level and life history changes caused by present climatic conditions with those changes caused by Pleistocene climatic fluctuations. This investigation will help us better understand the magnitude of the threat that the tiger salamanders are currently facing, and will greatly inform future conservation efforts.

The Snowmastodon field site provides a rare opportunity for such a study. There are few 100 ka Pleistocene records in North America, and fewer still that contain thousands of salamander fossils in a stratigraphic sequence spanning tens of thousands of years of environmental change (Rogers 1985). The site has excellent stratigraphic control, exceptionally preserved paleoenvironmental proxies such as plants and invertebrates, and a large and diverse vertebrate community comprised of extinct and extant high-elevation species. Analysis of the *Ambystoma* fossils at this field site will reveal a complete story of the life history dynamics of the species, with great temporal and spatial resolution, that will unite the findings of previous studies on the topic.

## The Species: *Ambystoma tigrinum*

*Ambystoma tigrinum* is ideal for a study on the impact of climate change on both individual life history and population level dynamics for several reasons. *Ambystoma* is capable of developmental growth plasticity in periods of environmental heterogeneity, altering their life history in response to changes in habitat permanence, population density, and competition for resources. In times of scare food supply or increased competition, some salamanders will become cannibalistic; this is manifest in the distortion of various skeletal elements that are preserved in the fossils. In addition to metamorphosing into terrestrial adults after an initial aquatic larval stage, *Ambystoma* can also become paedomorphic; they have the ability to maintain larval morphological traits and remaining aquatic while achieving sexual maturity. Paedomorphosis in the *Ambystoma* occurs through neoteny, in which normal physiological developments are delayed or halted. These two different life histories are reflected by measurable morphological differences that are preserved by the fossils. Paedomorphosis in *Ambystoma* is influenced by temperature and the presence of predator fish populations. It is more common in colder environments and in ponds that are more permanent than seasonal (McMenamin et al. 2010). Pond permanence is influenced by the rate of precipitation, and relative humidity. Thus, a morphological study of the *Ambystoma* fossil record is able to provide an unrivaled biological report on local climatic transitions.

## The Site: Snowmastodon Site, Colorado

Quality ecological records are crucial in paleoclimatological studies with biological proxies. However, there is often a tradeoff between the magnitude of the temporal scale and the preservation resolution of the fossil data. An ideal ecological record must span enough generations and geologic time to capture significant trends, while at the same time preserve enough detail of the morphological features that chronicle the climatic history: such a record was discovered in 2010 by construction workers near Snowmass Village, Colorado at an elevation of 2671 m.

The site is in an isolated lake basin that contains fossils deposited ~40,000 to ~100,000 years ago, during the later Pleistocene. Fossils discovered at the site include extinct megafauna (ground sloth, mastodon, bison, camel, mammoth), well-preserved plants, invertebrates (ostracods, gastropods, insects), and microvertebrates (fish, amphibians, reptiles, birds and mammals). With thousands of preserved fragments, the *Ambystoma* fossil record is one of the best represented at the site. The salamander bones represent paedomorphic and metamorphosed individuals of both the cannibalistic and non-cannibalistic forms. While fossils from the different units are preserved in varying states of articulation, all horizons contain salamander remains. Fully articulated specimens can be found in abundance within the pulp cavity of a mastodon tusk and in the sediment beds.

Preliminary field work on the biotic signatures of the horizons suggest a transition from warmer and moister to cooler and drier climatic conditions, though the timing, duration, and magnitude of these fluctuations remain unclear. An analysis of the size and morphological characteristics of *Ambystoma* is the best strategy for providing resolution to the local environmental history due to the unrivaled abundance and preservation of the *Ambystoma* record at this newly discovered field site.

## Preliminary Hypothesis

Since the Snowmastodon field site was recently discovered, no study has been published on the climatic transitions record by the stratigraphic sequence. With the assistance of Professor Hadly, I will maintain correspondence with the Denver Museum and other researchers working on samples from the site in the following months in order to acquire a working knowledge of the general environmental history of the region. I propose that changes in Pleistocene temperatures and rates of precipitation manifest in statistically significant changes in the size and morphological diversity of *Ambystoma* populations in the stratigraphic sequence. While the general mechanism for these changes will confirm previous studies on life history alterations in the *Ambystoma*, the magnitude of biotic responses will vary between that recorded by the Pleistocene fossil record and the study of extant populations in Yellowstone as described by McMenamin et al. (2008). I propose that the current threat facing *Ambystoma* populations in North America is of a magnitude that has not occurred in the historic past.

## Methods & Analyses

The *Ambystoma* fossils have been provided by the Denver Museum of Natural History as a loan to PI Elizabeth Hadly, in whose lab I will be working with the specimens. My study will be one of the first on this collection of fossil salamanders. To inform my project, I will use previous studies of *Ambystoma* fossils at other locales (Bruzgul et al. 2005, Holman 1980, McMenamin 2008, McMenamin and Hadly 2010, Rogers 1985, Tihen 1958) for methodologies, and plan to use comparative collections housed in Dr. Hadly's lab to assist me in my identifications. Though the fossils will include dentaries, skull bones, and various other fragments, I will use vertebral elements to test my hypothesis because they record metamorphic state and body size, which is informative of growth plasticity and changes in life history. Since different stratigraphic units are often subject to differences in preservation status and quality, I will need to determine the taphonomic consistency of the units, and will work closely with Professor Hadly, who has published extensively on this topic. I will sort fossils by skeletal element into intervals based on the stratigraphic units. Next, the number of identified specimens (NISP) and the minimum number of individuals (MNI) will be determined for each interval. The MNI can be determined by counting the number of sacral or cervical vertebrae present in each interval, since an individual only has one of each of these elements (Bruzgul et al. 2005). Body size will be obtained by measuring the centrum length and anterior width of each specimen (Tihen 1958). The age of each specimen can be determined by the morphological state of the neural arch: juvenile individuals have unfused neural arches, and old individuals have fused neural arches. The developmental state can be determined by the morphological state of the centrum: larval and neotenic individuals have unfused centra while terrestrial individuals have fused centra (Tihen 1958, Rogers 1985). All measurements will be collected with an electronic caliper, and when necessary, under a stereo microscope. At the end of data collection, I will compile a dataset in Excel of all the unique specimens within each interval. For each specimen, relative age, body size, and metamorphic state will be recorded. Standard morphometric statistics will be applied to determine whether there are significant differences in body size and metamorphic state and, if found, whether these differences are concordant with environmental reconstructions using other data from the site. All statistical analysis will be conducted using R, a statistical computing language. Finally, I will compare the results of my study with that of McMenamin et al. (2008) with the assistance of Professor Hadly, who was also involved in that previous study.

## Tentative Work Plan

Spring Quarter: I will familiarize myself with *Ambystoma tigrinum* morphology, biology, and population dynamics. I will delve into the background literature on the different life histories of these amphibians with Professor Hadly. After the initial background research, I will begin sorting the specimens into different intervals, and characterizing the bone elements. I expect to have the knowledge necessary to perform the bulk of my analyses for this project by the beginning of summer.

Summer Quarter: I plan to work on my project throughout the months of July and August, and in early to mid-September before school begins.

Week One – Two: I will finish sorting and identifying all the fossil vertebrae of interest.
Week Three – Seven: I will record the age and developmental state of all the fossil vertebrae.
Week Eight – Ten: I will spend the final weeks of summer analyzing my completed dataset using the software R.

Tentative Budget:

| Item Description | Requested Budget | Total Requested Budget |
|---|---|---|
| Student stipend | $560/ week for 10 weeks | $5,600 |
| | | |
| | | $5,600 |

**Works Cited**


Bruzgul, Judsen E, Webb Long, and Elizabeth A Hadly. "Temporal Response of the Tiger Salamander (*Ambystoma Tigrinum*) to 3,000 Years of Climatic Variation." *BMC Ecology* 5, no. 1 (September 13, 2005): 7.

Collins, James P, and Andrew Storfer. "Global Amphibian Declines: Sorting the Hypotheses." *Diversity and Distributions* 9, no. 2 (March 1, 2003): 89–98.

Holman, J. Alan. "Paleoclimatic Implications of Pleistocene Herpetofaunas of Eastern and Central North America." *Transactions of the Nebraska Academy of Sciences and Affiliated Societies* (January 1, 1980). http://digitalcommons.unl.edu/tnas/286.

———*Pleistocene Amphibians and Reptiles in North America*. New York: Oxford University Press, 1995.

McMenamin, Sarah K, and Elizabeth A Hadly. "Developmental Dynamics of *Ambystoma Tigrinum* in a Changing Landscape." *BMC Ecology* 10, no. 1 (April 3, 2010): 10.

McMenamin, Sarah K, Elizabeth A Hadly, and Christopher K Wright. "Climatic Change and Wetland Desiccation Cause Amphibian Decline in Yellowstone National Park." *Proceedings of the National Academy of Sciences* 105, no. 44 (November 4, 2008): 16988–16993.

Reading, C. J. "Linking Global Warming to Amphibian Declines Through Its Effects on Female Body Condition and Survivorship." *Oecologia* 151, no. 1 (September 21, 2006): 125–131.

Rogers, Karel L. "Facultative Metamorphosis in a Series of High Altitude Fossil Populations of *Ambystoma Tigrinum* (Irvingtonian: Alamosa County, Colorado)." *Copeia* 1985, no. 4 (December 10, 1985): 926–932.

Sprules, W. Gary. "The Adaptive Significance of Paedogenesis in North American Species of *Ambystoma* (Amphibia: Caudata): An Hypothesis." *Canadian Journal of Zoology* 52, no. 3 (March 1974): 393–400.

Stuart, Simon N, Janice S Chanson, Neil A Cox, Bruce E Young, Ana S. L Rodrigues, Debra L Fischman, and Robert W Waller. "Status and Trends of Amphibian Declines and Extinctions Worldwide." *Science* 306, no. 5702 (December 3, 2004): 1783–1786.

Tihen, J.A. "Comments on the Osteology and Phylogeny of *Ambystoma*tid Salamanders." *The Bulletin of the Florida State Museum, Biological Sciences* (1958).