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## *Research Accomplishments and Future Research Plans – August 2016*

How vital rates, life-history traits, and genetic diversity vary with climate, habitat, and population factors is central for our understanding of evolution of life histories, population dynamics, and risk of extinction in natural populations. I develop methods and test theory-based hypotheses on the determinants of variation in vital rates, life-history traits, and genetic diversity on exceptional long-term longitudinal dataset of salmonid species living in Slovenian streams and seabirds living in the Northeastern Pacific. I then integrate results and insights into life-history models to inform management of endangered populations, with particular focus on the effects of climate change on weather and climate extremes, and habitat variation.

More specifically, I use a mixture of empirical and statistically and mathematically sophisticated approaches to investigate:

- 1) Life-history and genetic adaptations to weather and climate extremes;
- 2) How early environment shapes the life histories of long-lived animals and their effects on population dynamics;
- 3) The determinants of genetic, life-history, and demographic variation within- and among populations of the same species.

These three lines of research and the model systems I use allow me to study the acute (1), delayed (2), and long-term (3) effects of climate and habitat variation on variation in vital rates, life histories, and population dynamics of animal species. I plan to submit grants for all three lines of research; my first grant proposal will be on life-history and genetic adaptations to weather and climate extremes.

### **1. Life-history and genetic adaptations to weather and climate extremes**

As climate change is predicted to increase the frequency and intensity of weather and climate extremes, tests on empirical data of theory-based predictions on the consequences of extreme events are necessary and urgent to provide a balanced view on the adaptive potential of species and the risks associated to all aspects of climate change. With climate change, species that have been never affected by extreme events are predicted to experience them either today or in the near future, and species that are already affected by extreme events are likely to experience more frequent and more intense extreme events.

A big challenge for empirical studies is that extreme events that result in strong demographic and genetic responses are, by definition, rare events. As a result, most of the empirical studies on the effect of extreme events have been opportunistic and anecdotal; for instance, limited information on the study system before the occurrence of the extreme event does not typically allow before-after comparisons, which are necessary to tease apart the effects of acute and long-term habitat and climate variation on vital rates and life histories.

I use marble trout (*Salmo marmoratus*) as a model system in this line of research. Salmonids have been often used as model systems in ecology and evolutionary biology, due to their vast geographic distribution, their ecological and life-history variability, and their strong genetic and plastic responses to habitat and climate variation. My collaboration on marble trout with field biologist Alain Crivelli of the Biological Station of Tour Du Valat (France) started in 2004. Marble trout live in Slovenian streams that are frequently affected by extreme flood events causing massive mortalities. Marble trout populations have surprisingly persisted for centuries, despite population sizes as low as a few dozen individuals, the occurrence of extreme climate events, little genetic variability, and no immigration from other populations.

Marble trout as a model system provides a unique opportunity to investigate the effects of extreme climate events on vital rates, life histories, and genetic diversity, thanks to the long-term monitoring and sampling of multiple populations, the collection of an exceptional dataset of demographic and genetic data at the individual level (monitoring and tagging is annual or bi-annual depending on the population), the occurrence of multiple flash floods and debris flows in the last 15 years, integration of field and lab data, and my deep knowledge of the system.

In my research, I found that flash floods caused habitat destruction and mortality or displacement of a large fraction of the population, with survival rates lower than 90% of normal survival rates [1]. However, in the years following the floods there was a substantial increase in early survival and growth of fish in the affected populations, mostly due to relaxation of the depressing effects of population density on vital rates [1], which in theory contributes to population recovery [2]. Furthermore, my colleagues and I were able to identify recurrent genetic bottlenecks in marble trout populations using

microsatellites [3]. We hypothesized that bottlenecks may have been caused by repeated flood events in the last centuries, and I am currently testing more fine-grained hypotheses on their frequency using Next-Generation Sequencing data.

Theory predicts genetic and life-history adaptations to extreme events, but whether those adaptations are short- or long-lived depends on the recurrence interval of the events and the life histories of the species [2]. In the next five years, I intend to combine long-term tag-recapture data, molecular pedigree reconstruction, and novel statistical and modeling methods to test theory-based hypotheses on the genetic and life-history consequences of extreme climate events, and to provide new elements to the overarching predictive framework for the study of the effects of extreme events on natural populations that I have been developing [2,4,5]. In particular, I intend to:

- (i) Develop pipelines for parentage assignment and then reconstruct pedigrees using panels of population-specific SNPs. Despite the increasing availability of algorithms and software, developing analytical ecosystems for small and highly inbred populations is intrinsically challenging and has broad value to biologists;
- (ii) Test the hypotheses of acceleration of life histories and higher variation in reproductive success after extreme events, and their consequences for the evolution of life-history traits and for genetic diversity;
- (iii) Identify candidate genes under selection using genotype-by-sequencing and outlier tests in before-after flood comparisons, and test the association between fitness and genotypes at the individual and family level;
- (iv) Modeling the temporal and spatial correlation of extreme events occurring in the region using the 1960-today data that I collected for more than 200 meteorological stations, and then model the eco-evolutionary dynamics of marble trout populations. The estimation of a correlation structure among extreme rainfall events in Western Slovenia that leverages information from hundreds of meteorological stations would provide a clearer picture of the past and future trends of extreme rainfall events and flash floods.

## **2. How early environment shapes the life histories of long-lived animals and their effects on population dynamics**

One of the most important effects of climate change is the increase in climate variability. With higher climate variability, early cues of future environmental conditions driving variation in life histories are likely to become less informative, in particular for long-lived animal species. It is thus crucial to investigate how higher climate and resource unpredictability would alter the adaptive value of early induced variation in life histories for long-lived species.

In this line of research, I have used kittiwakes (*Rissa tridactyla*) living in Middleton Island (Alaska) as a model system. Kittiwakes are long-lived seabirds that start breeding between 4 and 15 years old, live up to 20-25 years old, and have been used as a model system for studies on genetic and plastic adaptations to habitat variation, aging, seasonal migration, parental investment in offspring, and behavioral and life-history responses of top predators to variation in climate and prey availability.

My collaboration with field biologist Scott Hatch of USGS and physiologist Alexander Kitaysky of University of Alaska, Fairbanks on this model system started in 2011. In the Middleton colony, free-living kittiwakes were raised as chicks and later reproduced in nests in which the food available to parents and chicks was experimentally manipulated: in food-supplemented nests, parents and chicks received supplemental food during the breeding season, while in control nests no supplemental food was given to either parents or chicks. The return of experimental chicks to the colony to breed provides a unique opportunity to test hypotheses on how early environment shapes within-population variation in life-history strategies in a long-lived animal.

So far, I found younger age at first breeding for kittiwakes that experienced suboptimal natal conditions, as well as greater productivity of early recruiting kittiwakes that grew in control nests compared with those that grew in food-supplemented nests [6]. These results support the predictions of life-history theory of faster life histories in response to suboptimal conditions during development. I also found that favorable conditions at breeding increase reproductive success while delaying, but not avoiding, the viability selection that normally occurs during the nestling phase, with a net positive effect of early food supplementation on survival up to recruitment [7].

The monitoring of banded birds will continue for at least another 5 years and approximately 100 birds are expected to complete their life cycle throughout that time. With my colleagues, I plan to use a combination of laboratory analysis (e.g. analysis of variation in telomere length dynamics), statistical modeling of variation in life histories and vital rates, and forward simulations to investigate how environmentally driven food shortages and controlled increases in food availability during the neonatal and breeding stages might induce the adoption of slow- vs. fast-living life histories, as reflected in the onset of breeding, lifetime reproductive performance, aging, and survival, as well their effects on population dynamics.

### 3. Determinants of genetic, life-history, and demographic variation within- and among isolated populations

To understand how long-term within- and among-population variation in vital rates and life histories emerge, we need long-term studies that include episodic events and contrasting environmental conditions, data to characterize individual and shared variation, and statistical models that can tease apart shared and individual contribution to the observed variation in vital rates and life histories. I develop statistical methods and overarching modeling frameworks for the fine-grained estimation of vital rates, life-history traits, and their determinants when there is substantial individual and shared variation in those traits, using populations of marble (10 isolated populations), rainbow (5), and brown trout (1) living in Slovenian streams as model systems.

I recently developed a fast, general Empirical Bayes approach for the estimation of individual variation in growth of organisms, which also allows to predict unobserved individual growth trajectories [8]. In my current research, I am testing whether parameters of growth models estimated at the individual level can condense the information contained in size-at-age data when testing for selection on growth rates and size-at-age in natural populations. I am also investigating trade-offs between model complexity, biological interpretability of parameters, and goodness of fit in random-effects models of growth and survival [9].

The monitoring of the Slovenian marble, rainbow, and brown trout populations started in 1993; in total, more than 10,000 unique individuals have been tagged across populations, and more than 4,000 marble trout have been genotyped using SNP-assays. In addition to furthering our understanding of the effects of habitat variation on vital rates and life histories, my work has the goal to forecast future population size, age-, size-, and spatial structure and inform management of species under scenarios of climate change.

In my current and future research, I plan to use my novel statistical approaches and marble trout, rainbow, and brown trout populations as model systems to:

- (i) Tease apart the contribution of adaptation vs. genetic drift in determining genetic and phenotypic differences among small and isolated populations using classic genotyping, NGS-data, and genotype-by-sequencing;
- (ii) Test the effects of inbreeding on fitness and their variation among populations, motivated by the paradoxical observation that the most inbred marble trout population is also the one with the highest survival rates;
- (iii) Test the “individual-quality hypotheses” of a positive co-variation between survival and reproductive success, which is often found across taxa, although it is not predicted by life-history theory;
- (iv) Estimate variation among populations of heritability of life-history traits using a combination of controlled experiments in the fish farm and field data;
- (v) Integrate (ii)-(iv) and estimates of vital rates in life-history models to predict the demographic and genetic future of the populations, as well as to identify key pieces of empirical information that are required for advancing understanding and inform management. For instance, how many years of monitoring are needed to reach an asymptote in the amount of information on vital rates, life histories, and population dynamics that is useful for conservation?

#### References

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