

BIOGRAPHICAL SKETCH

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NAME: Bergland, Alan Olav

eRA COMMONS USER NAME (credential, e.g., agency login): bergland.alan

POSITION TITLE: Assistant Professor

EDUCATION/TRAINING (*Begin with baccalaureate or other initial professional education, such as nursing, include postdoctoral training and residency training if applicable. Add/delete rows as necessary.*)

INSTITUTION AND LOCATION	DEGREE (if applicable)	Completion Date MM/YYYY	FIELD OF STUDY
University of Oregon	B.S.	06/2004	Philosophy
University of Oregon	B.S.	06/2004	Biology (with Honors)
Brown University	Ph.D.	06/2010	Ecology and Evolution
Stanford University	Postdoctoral	04/2014	Biological Sciences
Stanford University	Research Assoc	12/2015	Biological Sciences

A. Personal Statement

My research program seeks to understand the adaptive evolution and genetic basis of life-history traits in response to ecologically relevant environmental variation. This integrative work uses a mixture of tools from field ecology, quantitative-, molecular-, and population-genetics, combined with rigorous statistical analyses. My initial training as an undergraduate was in field ecology, where I studied the role of larval nutrition and overwintering thermal stress on adult fitness components in the pitcher-plant mosquito, *Wyeomyia smithii*. Inspired by this work, as a Ph.D. student I investigated the genetic and physiological basis of phenotypic plasticity in female fecundity of *Drosophila melanogaster*. My PhD work entailed several very large phenotyping efforts (thousands of flies assayed and over a million eggs counted by eye) and identified one locus controlling natural variation in fecundity. While successful I nonetheless wanted to understand the evolutionary forces acting on many loci controlling natural variation in life-history traits. Accordingly, as a post-doc I studied the genetic basis of adaptive differentiation in *D. melanogaster* along latitudinal clines and among seasons. In 2016, I will be in a faculty position at the University of Virginia where my research program will utilize my diverse skill set to study the evolutionary history and genetic/physiological basis of natural variation in fitness related traits in a generalized and high-throughput way. Below, I list four publications that demonstrate my experience and qualifications for the proposed research.

As a post-doc I have developed independent collaborations with scientists throughout the world that complimented my main research projects. While this work is still in progress, I will briefly describe it here. In collaboration with Chris Balakrishnan (East Carolina University), Elaina Tuttle (Indiana State University), and others I have played a leadership role in examining the evolutionary history of a remarkable, stably balanced 100Mb inversion polymorphism in the White-Throated Sparrow. We show that this inversion, which is maintained at intermediate frequencies by near perfect disassortative mating, arose via adaptive introgression and has subsequently evolved much as neo-sex chromosomes do. I will continue to play a small role in this project as it continues to develop. A second independent research program I have become involved in is

studying the genetic basis of adaptive differentiation of phenotypic plasticity in *Daphnia pulex*. This work is in collaboration with Andrew Beckerman (Univ. of Sheffield, UK). In my research proposal, I describe how I will continue to work on this system in collaboration with Dr. Beckerman. Finally, in collaboration with Dmitri Petrov (Stanford) and Paul Schmidt (U Penn) I have spearheaded a large consortium of fly biologists throughout the US to collect flies on a seasonal basis near their home institutions and subsequently use these collections for whole-genome resequencing. This consortium met in 2012 at NESCent and in the subsequent years we have grown to over a dozen labs throughout the US. Our work has spurred similar efforts in Europe and I serve as a go-between for the US and European groups. Moving forward, I will continue to play a major role in this international collaboration.

I have been actively involved in mentoring students and I am committed to continuing this practice. At Stanford, I mentored >10 undergraduate students, post-grad research technicians, and graduate students. Many of these students completed honors theses or similarly in-depth, semi-independent research projects leading to one published MS and several others in preparation. The majority of these students have been minorities, women, or first-generation college students and I am committed to promoting gender, ethnic, cultural, and intellectual diversity in the sciences through continued mentorship. Three of these students have now entered PhD programs in Ecology/Evolution/Genetics at Harvard, UC Berkeley, and UC Davis.

Relevant Publications:

- Bergland AO**, E Behrman, K O'Brien, P Schmidt & D Petrov, 2014. Genomic evidence of rapid and stable adaptive oscillations over seasonal time scales in *Drosophila*. *PLoS Genetics* 10(11): e1004775.
- Paaby AB, **Bergland AO**, Behrman EL, Schmidt PS, 2014. An amino acid polymorphism in the *Drosophila* Insulin Receptor demonstrates pleiotropic and adaptive function in life-history traits. *Evolution* (68): 3395-3409
- Bergland AO**, Chae HS, Kim YJ & Tatar M, 2012. Fine scale mapping of natural variation in fly fecundity identifies neuronal domain of expression and function of an aquaporin. *PLoS Genetics* 8(4): e1002631
- Bergland AO**, Genissel A, Nuzhdin SV & Tatar M, 2008. Quantitative trait loci affecting phenotypic plasticity and the allometric relationship of ovariole number and thorax length in *Drosophila melanogaster*. *Genetics* 180: 576-582

B. Positions and Honors

Positions and Employment

- 2014 - 2015 Research Associate, Dept. of Biology, Stanford University, Stanford, CA
- 2016 - Assistant Professor, Dept. of Biology, University of Virginia, Charlottesville, VA

Other Experience and Professional Memberships

- 2004 - Member, Genetics Society of America (GSA)
- 2014, 2015 NSF DEB grant review panelist
- 2014, 2015 *Ad hoc* grant reviewer for BBSRC, INR, Austrian Science Foundation
- 2014 Post-doc representative for the GSA Awards Committee
- 2015 GSA 100-year Anniversary Committee

Honors

- 2007-2008 Oliver Cromwell Gorton Arnold Biological Fellow, Brown Univ.

C. Contribution to Science

1. Demonstrating the presence of polygenic adaptive oscillations over seasonal time scales. It is well known that adaptive evolution of highly quantitative traits can proceed rapidly in response to natural selection pressures. The genetic basis for such adaptive evolution has remained elusive and it has often been assumed the difficulty in identifying the genetic targets of natural selection is due in part to the genetic architecture of traits under selection. One standard model is that that rapid adaptive evolution of

quantitative traits is driven by small changes in allele frequency at a large number of loci with individually small effects. This assumption is referred to as the 'infinitesimal model' as is a foundational model in quantitative-genetics. This model plays a major role in shaping the Neutral Theory, the dominant framework of population-genetics. One consequence of this model is that identifying specific loci that contribute to rapid adaptive evolution of quantitative traits may be difficult, if not impossible.

Drosophila melanogaster undergoes rapid adaptive evolution in quantitative life-history traits over seasonal time scales. We sought to identify loci that underly this adaptive process by sampling flies over the course of three years in a temperate orchard during the spring and fall. Surprisingly, we identified hundreds of loci that shift dramatically in allele frequency between seasons, on average between 40 and 60% (Bergland *et al*, 2014). We have shown that these loci are enriched for functional genomic elements, respond predictably to an acute frost event, vary in a predictable way among populations arrayed along latitudinal clines, and are associated with measurable differences in stress tolerance phenotypes. We also showed that these so called "seasonal SNPs" are old. The vast majority of them predate the migration of flies out of Africa and are more likely than expected by chance to be polymorphic in *D. melanogaster's* sister species, *D. simulans*. This latter result suggests that seasonal SNPs may be millions of years old and possibly maintained at intermediate frequencies in the species by some balancing selection caused by environmental heterogeneity through time and space.

Importantly, this work has shown that many loci of large phenotypic and fitness effect do contribute to rapid adaptation in quantitative traits over very short time scales. We have also begun to examine the phenotypic effect of selected seasonal SNPs and have shown that their effects are measurable and highly pleiotropic (Paaby *et al*, 2014). Therefore, our work suggests that the infinitesimal model may not hold.

My work on rapid adaptation over seasonal time scales occurred while I was a post-doc and was performed in collaboration with Paul Schmidt (U Penn) and Dmitri Petrov (Stanford). I prepared sequencing libraries, analyzed all the high-throughput sequencing data, and developed forward simulations to demonstrate the plausibility of rapid adaptive evolution at hundreds of loci.

In addition to conceptually advancing our understanding of rapid adaptive evolution, this work fostered two technical advances in high-throughput sequencing. The first was the demonstration that pooled-resequencing is an accurate way to assess allele frequencies genome-wide (Zhu *et al*. 2012). The second was the development of software to estimate patterns of linkage disequilibrium from pooled resequencing data (Feder *et al* 2012).

- Bergland AO**, E Behrman, K O'Brien, P Schmidt & D Petrov, 2014. Genomic evidence of rapid and stable adaptive oscillations over seasonal time scales in *Drosophila*. *PLoS Genetics* 10(11): e1004775.
- Paaby AB, **Bergland AO**, Behrman EL, Schmidt PS, 2014. An amino acid polymorphism in the *Drosophila* Insulin Receptor demonstrates pleiotropic and adaptive function in life-history traits. *Evolution* (68): 3395-3409
- Feder A, Petrov D & **Bergland AO**, 2012. LDx: Estimation of linkage disequilibrium from high-throughput pooled resequencing data. *PLoS ONE* 7(11): e48588
- Zhu Y, **Bergland AO**, Gonzalez-Perez J & Petrov D, 2012. Empirical validation of pooled whole genome population re-sequencing in *Drosophila melanogaster*. *PLoS ONE* 7(7): e41901

2. Uncovering the role of historical admixture in generating clinal variation in *D. melanogaster*.

D. melanogaster has long served as an important model for studying local adaptation. Largely, work on local adaptation in this system has focused on examining patterns of genetically based phenotypic variation along latitudinal clines. For historical reasons, this work has primarily focused on latitudinal clines in North America and Australia. Genetically based phenotypic clines and many clines in allele frequency are parallel between these two continents which were colonized by *D. melanogaster* in the last several hundred years. Parallel clinality has been taken as strong evidence of local adaptation.

By examining genome-wide estimates of allele frequencies in a world-wide sample of flies, I showed that these parallel clines were likely generated by the colonization history of flies and not necessarily spatially varying selection. Notably, my work showed that both North America and Australia likely represent secondary contact zones between European and African lineages of flies and that this process generated clinal variation across a large fraction of the genome. This finding, therefore, dramatically shifts our understanding of a well studied and classic system in evolutionary biology.

My work on clinal variation in *D. melanogaster* occurred while I was a post-doc. I collected fly samples, generated sequencing libraries, performed all the statistical analysis.

Bergland AO, Tobler R, González J, Schmidt P & Petrov D. Secondary contact and local adaptation contribute to genome-wide patterns of clinal variation in *Drosophila melanogaster*. In review, Molecular Ecology; preprint available at bioRxiv: 009084

3. Identifying the physiological and genetic basis for natural variation in life-history traits.

The life-history of an individual - its age-specific patterns of reproduction and survival - determine population growth rate and demographic fitness. Thus, life-history traits are likely to be subject to strong selective pressures in the wild (Bergland 2011). Despite their central importance in evolutionary biology, the genetic basis for natural variation in life-history traits has remained elusive.

During my Ph.D. I performed two extensive QTL mapping experiments seeking to identify the genetic basis of life history traits in *D. melanogaster*. One broader study described a complex genetic architecture underlying natural variation in ovary- and body-size (Bergland et al 2008). In a second study, I mapped natural variation in fecundity to a single gene *Drip* (Bergland et al 2012). This gene encodes for an aquaporin that allows for efficient transport of water and (possibly) small solutes across cell membranes. Aquaporins are highly expressed in the malpighian tubules, the insect equivalent of the kidney. Surprisingly, I found that *Drip* was differentially expressed between high- and low- fecundity strains in ~12 neurons in the brain and modulate fecundity through an endocrine pathway involving both dopamine and corazonin. Ultimately, this work identified a new gene that affects fecundity and linked it to a physiological pathway. The limitation of this work was that I had no idea whether this mutation was segregating at intermediate frequencies due to balancing selection or if it was a rare mutation that was unconditionally deleterious. The drive to answer this question led to my post-doc work which I described above.

Bergland AO, Chae HS, Kim YJ & Tatar M, 2012. Fine scale mapping of natural variation in fly fecundity identifies neuronal domain of expression and function of an aquaporin. PLoS Genetics 8(4): e1002631

Bergland AO. Mechanisms and ecological genetics of reproduction in Dipteran insects, 2011. In *Molecular mechanisms of life history evolution*, eds. Flatt, T. & A. Heyland. Oxford University Press, Oxford, UK

Bergland AO, Genissel A, Nuzhdin SV & Tatar M, 2008. Quantitative trait loci affecting phenotypic plasticity and the allometric relationship of ovariole number and thorax length in *Drosophila melanogaster*. *Genetics* 180: 576-582

My publication list can be found here: <http://www.ncbi.nlm.nih.gov/pubmed/?term=bergland+ao>

D. Research Support

Ongoing Research Support

N/A

Completed Research Support

F32 GM097837-01

Bergland (PI)

04/01/2011-03/31/2014

Genomics of Natural Populations

The goal of this project was to (1) assess the accuracy of population based pooled resequencing on genome-wide estimates of allele frequencies and to apply this technique to investigate the evolutionary forces shaping

patterns of genetic variation among populations of *D. melanogaster* (2) sampled along latitudinal clines and (3) among seasons.

Stanford CEHG trainee research grant Bergland (PI) 09/01/2013-08/31/2015

Physiological Mechanisms Underlying Rapid Adaptive Evolution

The goal of this project was to test the hypothesis that hormonal genes underlie the tradeoff between somatic maintenance and reproductive output and are differentially expressed between winter- and summer- adapted flies.

NESCent Catalysis Grant Bergland, Petrov, Schmidt (multi-PI) 04/2012

Tracking the Biotic Response to Global Climate Change Through Genomic Analysis

The main goal of meeting grant was to initiate a collaboration amongst a diverse set of scientists to study the evolutionary genomics of *Drosophila* spp. in response to global climate change