OMB No. 0925-0001 and 0925-0002 (Rev. 03/2020 Approved Through 02/28/2023)

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 |

**A. Personal Statement**My research program examines the evolutionary dynamics of natural genetic variation in fitness related traits. We ask questions about the provenance and stability of polymorphisms that underlie functional genetic variation, and test how these polymorphisms adaptively track to spatial and temporal variation in selection pressures. This work seeks to assess the nature of balancing selection, and the importance of balancing selection as an evolutionary force which promotes diversity within populations and species. We address these questions using *Drosophila* and *Daphnia.* Due to their rapid development time, these assemblages of broadly distributed species have multiple generations per year (~10-20), enabling us to study their evolutionary dynamics in real-time and across a varied spatial landscape. Our work on *Drosophila* focuses on the genetic basis of local adaptation to seasonal and latitudinal variation in climate and nutrition. Our work on *Daphnia* examines the recurrent seasonal evolution of sexual investment, the mutational variance of predator induced plasticity, and the role of mating systems on the generation and maintenance of fitness-related diversity. In our research, we combine field-work, genomic analysis, and large-scale phenotyping efforts along with computational and experimental tools that we develop to gain insight into the basic evolutionary forces that maintain diversity.

I have always been drawn to the study of the evolutionary genetics of life-history traits. 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 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 the physiological details of this QTL were interesting (Bergland et al 2012), the evolutionary forces acting on it were unclear. Even if discernable, it is also unlikely that the specific strength of these forces at this locus were representative of the many loci controlling natural variation in life-history traits. To gain a more general understanding of the evolutionary forces acting on fitness related traits, as a post-doc I studied the genetic basis of adaptive differentiation in *D. melanogster* along latitudinal clines and among seasons. Using population genomic data, I showed that fly populations living in orchards adaptively evolve over seasonal time-scales (Bergland et al 2014). This work, and subsequent follow-up on additional populations (Machado, Bergland et al 2019), provides evidence that there are many, perhaps thousands, of common polymorphisms in the genome which vary in frequency between seasons, repeatedly across years and across geographic localities. The functional consequence of these adaptive polymorphisms remains elusive, as are the demographic forces that contribute to seasonal evolution in this species. By understanding these attributes in more detail, we will gain a deeper understanding of the role of temporal variation in selection pressures as a mechanism of balancing selection.

In 2016, I began a faculty position at the University of Virginia. My research group (total: 3 post-docs, 6 PhD students, 3 technicians, 2 undergraduate Honors students, ~20 undergraduate research students), has pursued basic questions about the nature and dynamics of functional variation within species. This work utilizes two organisms, Drosophila and Daphnia, to examine the genetic architecture of standing variation and to map that genetic architecture onto the dynamic changes in allele frequency that we observe through time. The ultimate goal of this work is to characterize the importance of environmental variation in the generation and maintenance of diversity within species. Working on these two organisms simultaneously has been very satisfying: logistically they complement each other and many tools can be shared among them; yet, they offer fruitful intellectual contrast, particularly with respect to the importance of sexual systems in the structuring of genetic variation. For both species, we have established long-term field sites for sample collection, experimental lab- and field-based mesocosms facilities, genomic resources, and experimental and computational to measure the genetic architecture of fitness-related traits across a range of environmental conditions (Erickson *et al* 2020).

I take the training of mentees in my lab very seriously and work closely with people to develop their projects. This training covers aspects of writing and presentation, statistical and computational analysis, and professional development. Mentees from my lab have been awarded fellowships, received small grants from the University and professional societies, and won presentation awards at both the regional and national levels. I have also instilled a training environment where senior members of the lab (at any rank) work to train and mentor more junior people. One post-doc from my lab has gone onto a faculty position (at University of Richmond), one graduate student has gone onto a post-doc (NIH), three undergrads/post-bacs have gone onto Evolutionary Biology PhD programs (UC Berkeley, Yale, UVA).

In addition, I have participated actively as a member of the Drosophila population genetics consortium, DrosEU (<http://www.droseu.net>). As a member of this consortium, I have been involved in generating a concatenated dataset of allele frequency estimates from >275 populations world-wide. We have developed a flexible pipeline to add new samples easily to this growing dataset and have coupled these samples with weather data prior to sampling, geographic location, and other sampling metadata. The updated version of this data-set is described here: <https://github.com/alanbergland/DEST/>

For the last 3 years, I have taught a course titled “*Molecular Evolution: diversity, mutants, and the biological myth of race*”. This seminar based-course teaches the mathematical foundations of population genetics and also addresses the societal impact that biologists have had in ascribing value (i.e.., superiority and inferiority) to diversity within our own species.

Relevant Publications:

**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**, 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.

Machado\* H, **Bergland AO\*,** Taylor R, Tilk S, Behrman E, Dyer K, *et* al. 2019. Broad geographic sampling

reveals predictable and pervasive seasonal adaptation in Drosophila. *bioRxiv: 337543v2*

Erickson PA, Weller CA, Song DY, Bangerter-Black A, Schmidt PS, **Bergland AO**. Unique genetic signatures

of local adaptation over space and time for diapause, an ecologically relevant complex trait, in *Drosophila*

*melanogaster*. In review. bioRxiv: *2020.05.06.081281v1*

<https://www.ncbi.nlm.nih.gov/myncbi/alan.bergland.1/bibliography/public/>

## ****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)

2016 - Member, Society for the Study of Evolution (SSE)

2014, 2015, 2016 NSF DEB grant review panelist

2014-2020 *Ad hoc* grant reviewer for BBSRC, INR, Austrian Science Foundation, SNSF, NWR, NSF-DEB

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 University

2020 Dept. of Biology Distinguished Teaching Award, University of Virginia

**C. Contributions to Science**

**1.** Local adaptation over seasonal time-scales. Organisms living in temperate environments experience dramatic changes in selection pressure across seasons. For species with many generations per year, rapid adaptive evolution can occur in response to temporal variation in the strength and direction of natural selection. Such adaptive tracking drives heritable phenotypic change through time, in principle caused by temporal changes in allele frequency at functional polymorphisms. Whether adaptive tracking through time is a major evolutionary process occurring within populations has remained an open question, and therefore the importance of temporal variation in selection pressures as a mechanism of balancing selection has remained elusive.

We have demonstrated that *D. melanogaster* adaptively evolves in response to environmental changes that occur across seasons, repeatedly over multiple years, and across multiple localities. Using population-genomic data, we have demonstrated that many loci in the genome change in frequency between seasons. Initial analysis (Bergland et al 2014) focused on a single population in Pennsylvania and identified hundreds of fluctuating polymorphisms; these loci were enriched for various functional annotations and are spread throughout the genome, suggesting polygenicity. We have extended this work (Machado\*, Bergland\*, et al 2019) to test whether adaptive evolution is a generic feature of fly populations caused by shifts at a common set of loci. Through collaboration with fly biologists throughout North America and Europe, we have examined genome-wide patterns of allele frequency change between seasons at over 20 localities. We demonstrate that there are a common set of loci which change in frequency throughout *D. melanogaster*’s range, and that change in frequency of these loci may be driven by localized variation in climate. We show that these seasonal polymorphisms are old, being generally present in ancestral African populations, and occasionally found to be segregating in the sister species, *D. simulans*.

Fly populations sampled at different times of year often (but not always) show heritable differences in a suite of life-history, stress tolerance, and morphological traits. In general, the view is that selection pressures over the winter select for individuals that allocate more resources into somatic maintenance than reproductive output; *vice-versa* in the summer. In some cases, we have been able to link specific seasonally varying polymorphisms to genetically based phenotypic variation observed among flies sampled in different seasons (Paaby et al 2014). We have argued that polygenic genetic variation along this life-history tradeoff can be stably maintained despite fluctuating selection, and that allele frequency fluctuations underlying this tradeoff can be large, given certain features of the genetic architecture of traits (Wittmann *et al* 2017).

We have extended our analysis of the temporal dynamics of seasonal evolution to a new system, *Daphnia pulex*. This species provides an important contrast to our work on Drosophila because it allows us to assess the role of mating systems and population dynamics on the maintenance of functional variation. Daphnia are facultative and tend to have small effective population sizes, therefore occupying the other end of the life-history spectrum, relative to Drosophila. Yet, this species is similar to Drosophila in that populations undergo multiple generations per year, and evolve across seasonal time-scales. I discuss our recent advances in studying the temporal dynamics of adaptation in Daphnia in the Research Proposal.

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

Wittmann MJ, **Bergland AO**, MW Feldman, PS Schmidt, DA Petrov. 2017. Segregation lift: A general

mechanism for the maintenance of polygenic variation under seasonally fluctuating selection. PNAS. doi:

10.1073/pnas.1702994114

Machado\* H, **Bergland AO\*,** Taylor R, Tilk S, Behrman E, Dyer K, *et al*. 2019. Broad geographic sampling

reveals predictable and pervasive seasonal adaptation in Drosophila. bioRxiv: 337543v2

2. The genetic architecture of natural variation in fitness related traits. All population harbor standing genetic variation in fitness. Whether this variation occurs because of stochastic processes (such as mutation, migration or drift) or by some form of balancing selection remains a fundamental question in evolutionary biology. Addressing this question is important because whether one set of forces are dominant to the other changes out interpretation about the nature of variation and the value of diversity. Assessing the extent of various evolutionary forces on acting on genomes is necessary for accurate interpretation of the evolutionary history of species, and for predicting future evolutionary change.

My work has sought to address this question by mapping natural genetic variation of fitness related traits, and subsequently testing how those polymorphisms change in frequency through time and space. In flies, we have approached this problem using an outbred mapping scheme (Weller and Bergland 2020). This approach utilized a multi-parental population founded by a limited number of genomes. We have developed a pipeline to reconstruct genomes from individual flies using <0.05X coverage, and show that this mapping approach is preferable to some alternatives in a number of important ways. We have applied this approach to study the genetic architecture of temperature-dependent diapause in *D. melanogaster* (Erickson et al 2020). We find that polygenic variation associated with diapause is predictably arrayed across a north-south cline; however, variation between seasons across multiple populations is idiosyncratic. Consistent with Machado, Bergland *et al* (2019), this work suggests that strong and idiosyncratic selection pressures occur between seasons, raising the possibility that much more of the genome is affected by seasonal evolution than previously estimated.

Daphnia provide a unique system to study the genetic architecture of fitness related variation as it evolves over seasons. The small Daphnia populations that we study are effectively wild multi-parental populations, in which recombinant siblings undergo clonal selection across the growing season. This dynamic allows us to perform QTL-mapping in wild populations and directly assess their change through time, in both natural and experimental settings. We are performing such work by focusing on natural polymorphism in sexual investment, and predator induced developmental plasticity. In the Research proposal, I discuss our recent advances studying the genetics of Daphnia populations.

Weller CW & **Bergland AO**. 2020. Accurate, ultra-low coverage genome reconstruction and

association studies in Hybrid Swarm mapping populations. In review. bioRxiv: 671925v2

Erickson PA, Weller CA, Song DY, Bangerter-Black A, Schmidt PS, **Bergland AO**. 2020. Unique genetic

signatures of local adaptation over space and time for diapause, an ecologically relevant complex trait, in

*Drosophila melanogaster*. In review. bioRxiv: *2020.05.06.081281v1*

**3.** The physiological and molecular basis of life-history variation. Identifying the genetic basis of natural variation is important for identifying novel mutations that provide insight into the basic biology of the organism. Much of my work has focused life-history traits, such as reproductive capacity, or various aspects of stress tolerance as mediated by the nutritional environment. These traits are important to focus on because they are central to understanding life-history tradeoffs via resource allocation (Bergland 2011).

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.

**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

**D. Additional Information: Research Support and/or Scholastic Performance**

## Ongoing Research Support

R35 GM119686 Bergland (PI) 05/01/2016-04/30/2021

*The genetic and physiological architecture of rapid and cyclic adaptation*

The goal of this project was to examine the genetic basis of rapid adaptive evolutionary change in two distinct species that are subject to different types of selection pressures in the wild. This work sought to identify functional polymorphisms affecting expression and phenotypes, and to study the change in frequency at these loci though time.

## Completed Research Support

None in the last 3 years.