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SPATIO-TEMPORAL ECOLOGICAL AND EVOLUTIONARY DYNAMICS IN NATURAL BUTTERFLY POPULATIONS (2013 FIELD SEASON)



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♦ INTRODUCTION

The study of evolution in natural populations has advanced our understanding of the origin and maintenance of biological diversity. For example, long term studies of wild populations indicate that natural selection can cause rapid and dramatic changes in traits, but that in some cases these evolutionary changes are quickly reversed when periodic variation in weather patterns or the biotic environment cause the optimal trait value to change (e.g., Reznick et al. 1997, Grant and Grant 2002). In fact, spatial and temporal variation in the strength and nature of natural selection could explain the high levels of genetic variation found in many natural populations (Gillespie 1994, Siepielski et al. 2009). Long term studies of evolution in the wild could also be informative for biodiversity conservation and resource management, because, for example, data on short term evolutionary responses to annual fluctuations in temperature or rainfall could be used to predict longer term evolution in response to directional climate change. Most previous research on evolution in the wild has considered one or a few observable traits or genes (Kapan 2001, Grant and Grant 2002, Barrett et al. 2008). We believe that more general conclusions regarding the rate and causes of evolutionary change in the wild and selection's contribution to the maintenance of genetic variation could be obtained by studying genome-wide molecular evolution in a suite of natural populations. Thus, we have begun a long term study of genome-wide molecular evolution in a series of natural butterfly populations in the Greater Yellowstone Area (GYA). This study will allow us to quantify the contribution of environment-dependent natural selection to evolution in these butterfly populations and determine whether selection consistently favors the same alleles across space and through time.

The focal species, *Lycaeides idas*, is one of five nominal species of *Lycaeides* butterflies that occur in North America (Figure 1; Nabokov 1949, Guppy and Shepard 2001, Gompert et al. 2006). These species are descended from one or more Eurasian ancestors that colonized North America about 2.4 million year ago (Vila et al. 2011). *Lycaeides idas* hybridizes with a second species, *L. melissa*, in the GYA (Gompert et al. 2010, 2012). *Lycaeides idas* is a holarctic species that is found in Alaska, Canada, and the central and northern Rocky Mountains of the contiguous USA (Scott, 1986). *Lycaeides idas* is univoltine and adults generally fly from mid-July to early August. In the GYA *L. idas* populations often occupy mesic forest and montane habitat at elevations ranging from 2000-3500 m above sea level. Most populations of *L. idas* in the GYA feed on *Astragalus miser* as larvae, but some populations feed on other native legumes (most notably, other species of *Astragalus* and *Lupinus*; Gompert et al. 2010). We selected *L. idas* as the focal species for this study because of our experience with this species, extensive data on the location and natural history of *L. idas* populations, the availability of genomic resources for this species, and several key aspects of this species's natural history (e.g., *L. idas* have non-overlapping generations with one generation per year, well-defined populations, and modest genome sizes, and *L. idas* are found in various different habitats that might experience different environment-dependent selection pressures).

The specific goals of this study are to: (i) quantify genetic variation and molecular evolution in *L. idas* and their relationship with population size and environmental variation across space (i.e., different populations) and through time (i.e., from generation to generation), and (ii) test the hypothesis that the nature and strength of environment-dependent selection varies among populations and over generations and

that this variation is sufficiently large to contribute to the maintenance of genetic variation in *L. idas*. This report documents the results from the second year of this study (2013), during which time we continued collecting *L. idas* for DNA sequencing and distance sampling to estimate population sizes (population size is an important parameter for our evolutionary models).

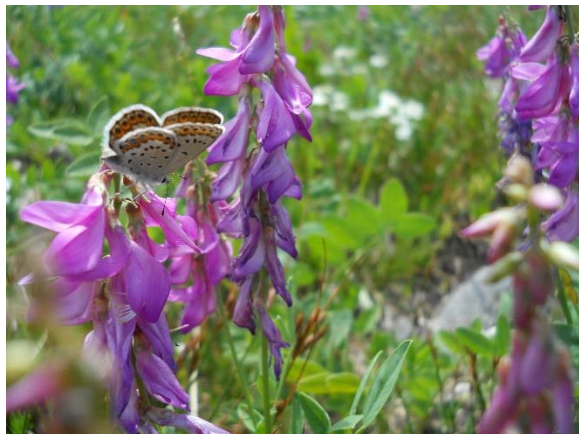


Figure 1. Photograph of a *L. idas* butterfly perched on its host plant (*Hedysarum*) on Rendezvous Mountain.

◆ METHODS

We began this long-term study in July of 2012. This report covers the second year of the study: July and August 2013. We collected 524 adult *Lycaeides idas* butterflies from 10 locations (Table 1). We are storing these whole adult butterflies at -80°C for DNA extraction and sequencing. In addition, we conducted a pilot study to evaluate a distance sampling protocol to estimate adult population densities and sizes in *L. idas*. Distance sampling involves counting individuals and recording their distance from a transect line or point (Buckland et al. 2001). This distance information is used to estimate a detection function that accounts for imperfect detection away from the transect line. We included four sites in this study: Bull Creek (BCR), Blacktail Butte (BTB), Bunsen Peak (BNP), and Garnet Peak (GNP). We randomly designated 10, 100-meter linear transects at each of the four sites (Figures 2 and 3). Two trained observers (ZG and LKL) slowly walked along each transect (about one pace per second) and measured and recorded the distance of each observed *L. idas* perpendicular to the transect line. We also observed and recorded the sex of each butterfly and the presence or absence of the larval host plant (*Astragalus miser*) near the transect line. We conducted these population surveys from July 6th until July 30th, and we only performed transect counts between 10:00 am and 2:00

pm under sunny or partly sunny skies. We visited BTB three times to quantify variability in population size over the flight season.

We estimated population densities (adult butterflies per square kilometer [km²]) using the *distsamp* function in the *unmarked R* package. We binned the detection distances of butterflies into 1-meter bins prior to analysis (e.g., 0 to 1 m, 1 to 2 m, etc.). We used a half-normal detection function and estimated the detection function and density model parameters using maximum likelihood (Royle 2004). This model assumes the latent transect-level abundance distribution is Poisson and that the detection process is multinomial with a different detection probability for each distance class or bin.



Figure 2. Photograph of a transect for distance sampling. The white line is the transect line and yellow flags indicate the location of observed *L. idas* butterflies.

◆ RESULTS

We observed and recorded distances for 122 butterflies across the four sites and 40 linear transects. Based on these observations our estimates of adult *L. idas* population density were: 0.00896 butterflies per square meter (standard error [se] 0.00196) at BCR, 0.00308 butterflies per square meter (se 0.00103) at BNP, 0.00528 butterflies per square meter (se 0.00153) at GNP, and 0.00241 (visit 1), 0.00415 (visit 2) or 0.00428 butterflies per square meter at BTB (se 0.00101 to 0.00154). We converted these density estimates to estimates of peak census population size based on rough estimates of each population's range (we identified suitable habitat from ground surveys and satellite images). Peak population size estimates were 793 butterflies (BCR), 211 butterflies (BNP), 373 butterflies (GNP), and 165-292 butterflies (BTB).

Because adult *L. idas* eclose (i.e., emerge following pupation) over a period of several weeks, these peak population size estimates are underestimates of the total adult population size at each site (perhaps by a factor of about three or four times given a one month flight season and a rough estimate of adult survival time in the wild of seven to ten days). We obtained peak population size estimates in 2012 that were higher on average than those from 2013: BCR = 794 butterflies, BNP = 721 butterflies, BTB = 2375 butterflies, and GNP = 206 butterflies.

Table 1. Population identification, locations, and number of adults (m = male, f = female) collected at each site for DNA sequencing. Sites within National Park boundaries are noted (GTNP = Grand Tenon National Park, YNP = Yellowstone National Park).

Population	Latitude	Longitude	Sample size
Blacktail Butte (GTNP)	43° 38' N	110° 41' W	25 m, 25 f
Bull Creek	43° 18' N	110° 33' W	34 m, 20 f
Bunsen Peak (YNP)	44° 56' N	110° 43' W	25 m, 25 f
Garnet Peak	45° 26' N	111° 13' W	37 m, 28 f
Hayden Valley (YNP)	44° 41' N	110° 29' W	25 m, 25 f
Mt. Randolph	43° 51' N	110° 24' W	40 m, 10 f
Periodic Springs	42° 45' N	110° 50' W	41 m, 10 f
Rendezvous Mountain (GTNP)	43° 36' N	110° 53' W	25 m, 25 f
Ski Lake	43° 31' N	110° 55' W	23 m, 29 f
Upper Slide Lake	43° 35' N	110° 20' W	40 m, 11 f

◆ DISCUSSION

Because we have just begun this long-term study and we have not yet sequenced the DNA from the sampled butterflies, we cannot yet make any conclusions about the rates or causes of molecular evolution in these study populations. But we have already learned a few things from the distance sampling surveys and analyses over the past two years.

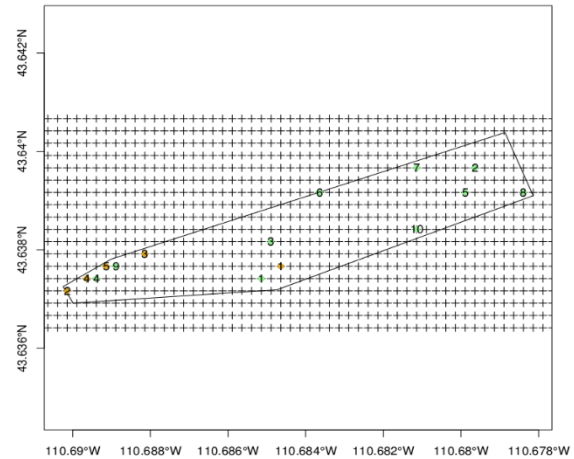


Figure 3. This plot shows the approximate boundary of the *L. idas* BTB population and the start points of transects (numbers and colored points). The cardinal or ordinal direction for each transect was chosen randomly but with the constraint that transect lines could not cross or leave the polygon boundary.

These initial analyses indicate that the four focal sites sustain adult *L. idas* populations of hundreds to thousands of individuals. These are the first population size estimates for this butterfly species. Based on these moderate population size estimates we predict that both genetic drift and selection are important drivers of evolution in this system (Lynch, 2007). The lower population size estimates in 2013 than 2012 are potentially interesting and could reflect demographic variability between years, but could also be an artifact caused by a change we made in how we designated transects. We also observed variation in the population size at BTB over the course of the summer, in particular our estimate from the first visit was about half that of the second and third visits. This is not surprising as the first visit was early in the season, and thus before the peak size. The consistency of the population size between the second and third visits (which were separated by about 10 days) indicates that the population remains at its peak size for more than a week.

We will continue this study during the 2014 summer field season. During this and subsequent field seasons, we will collect samples and estimate population sizes at all 10 sites listed in Table 1. We will also begin collecting weather and habitat data that will be useful for fitting causal models of molecular evolution. We plan to begin DNA sequencing of the collected *L. idas* after one or two additional field seasons.

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