RAPID EVOLUTION AND POPULATION DIVERGENCE IN RESPONSE TO ENVIRONMENTAL CHANGE IN *COLIAS* BUTTERLIES

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ABSTRACT

Jessica Keppel Higgins: RAPID EVOLUTION AND POPULATION DIVERGENCE IN RESPONSE TO ENVIRONMENTAL CHANGE IN *COLIAS* BUTTERLIES
(Under the direction of Joel Kingsolver)

My dissertation focuses on how environmental change, specifically in temperature and host plants, can drive physiological and morphological differences. I took advantage of historical studies with the *Colias* system of butterflies to assess adaptation and plasticity in larval performance in response to climatic change and changing host plant abundance. I have found that changing temperatures have affected the adaptation of some larval traits but not others. Specifically, as temperature variability has increased in both California and Colorado populations of *Colias,* the larval feeding rate has shifted to correspond to the new environmental conditions. Next, I studied how two Colorado populations of *Colias eriphyle* cope with repeated exposures to sub-lethal high temperatures simulating multi-day heat waves. I found that the higher elevation population suffered less detrimental fitness effects than the lower elevation population in regards to both short term (heat shock gene expression) and long term (overall growth rate) fitness effects. Building on my interest of how temperature and temperature variation affects multiple life stages I studied the effects of temperature during the pupal life stage on survival, growth and the resultant adult wing morphology. Generally, high temperatures decreased pupal time and less melanic adult wings. Finally, I used the two populations of *C. eriphyle* to quantify thermal performance differences of fitness when

larvae consume different host plants at two temperatures. I found that cooler temperatures increased the difference in performance between populations consuming different host plants and that thermal performance differs between populations. My research shows that temperature can affect fitness across many life stages and organisms have responded to these changes in temperature over time by adaptation.

To my mother who always inspired me to never stop learning.

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CHAPTER 1: OVERVIEW

Populations evolve traits that frequently yield a fitness advantage in their local environment, resulting in local adaptation (Williams 1966). Local adaptation to environmental conditions generates and maintains diversity among populations and species (Levene 1953). Organisms can be locally adapted to both abiotic factors such as climate and to biotic conditions such as competition, host plants, prey and/or natural enemies.

Temperature affects virtually all biological processes and systems in ectothermic organisms. Populations of the same and closely related species are often adapted to the local climatic conditions that they experience, resulting in clines in many phenotypic and morphological traits along latitudinal and elevational gradients. Local adaptation can also be seen on small spatial scales along elevational gradients has many taxa for a variety of traits, including phenology (Hodkinson 2005), morphology (Roland 1978), body size, behavior (Dingle, Mousseau & Scott 1990), thermal performance, and thermal tolerance (Damme *et al.* 1989; Stevens 1992; Gaston & Chown 1999; Badyaev & Ghalambor 2001). A major determinant of these local climates is temperature. In addition to temperature, insects can also be adapted to specific host plants or families of host plants. Local adaptation of insects to host plants is driven by aspects of host plant quality including abundance, plant defenses, and plant nutrient levels (Fox, Waddell & Mousseau

1994; Jongsma & Bolter 1997; Egan & Ott 2007). Herbivore populations may utilize and adapt to novel host plants that are introduced into their range.

Humans are changing the environment in many ways that are having interesting and diverse effects on organisms. As anthropogenic climate change increases both mean temperature as well as variability in climate and temperature, these novel conditions will present adaptation challenges for organisms (Easterling et al. 2000; IPCC 2007). For holometabolic organisms the effects of climate change may have both short and long-term effects that affect each life stage differently (Kingsolver, Arthur Woods et al. 2011).

Local adaptation of thermal optima is common across latitude and elevations (Huey & Kingsolver 1993; Cunningham & Read 2003; Sun & Friedmann 2005), however, ectotherms that were once adapted to their limited temperature range may now be experiencing fitness consequences as global mean temperature is increasing. The increasing temperatures along with the fact that upper thermal limits of performance in terrestrial ectotherms do not vary with elevation or latitude (Addo-Bediako, Chown & Gaston 2000; Sunday, Bates & Dulvy 2011) makes performance at temperatures above an organism's current thermal optima and below their upper thermal limits particularly interesting to study.

Human agriculture also changes the diversity and availability of host plants. Recent studies have demonstrated that evolutionary responses to novel host plants can occur quite rapidly, both for invasive plants (Harvey *et al.* 2010) and agricultural crops (Hare 1990; Gray *et al.* 2009). The interaction of temperature with other biotic factors such as availability and preference of certain foods can also affect local adaptation. Several herbivorous insects have demonstrated that host plant and rearing temperature

can interact to positively or negatively influence larval growth and development (Pelini *et al.* 2009; Diamond & Kingsolver 2012; Clissold, Coggan & Simpson 2013).

For my dissertation I want to know how populations are adapting to environmental change specifically changes in climate, host plants, and the interaction both. Overall, temperature and host plant choice are extremely important factors in understanding and exploring fitness differences across different populations and by using the *Colias* butterfly system I am able to elucidate some of the ways that temperature, changes in temperature, the availability of host plants, and how temperature and host plants interact can influence population fitness.

Colias butterflies have served as a model system for studying thermal adaptation for over 50 years (AE 1958; Hoffmann 1978). *Colias* adult butterflies and their thermal adaptation specifically regarding wing morphology is well characterized (Watt 1968; Kingsolver & Watt 1983; Kingsolver 1983; Ellers & Boggs 2002). However, little is known about *Colias* larvae and their local adaptation to climate (Sherman & Watt 1973). Additionally, *Colias* are generalists that feed on many plants in the *Fabaceace* family, however the distribution of genera is varied across their range. There is historical evidence suggesting that there is rapid local adaptation to host plant and local temperature (Sherman & Watt 1973; Tabashnik 1983) making the *Colias* system an attractive one to use to examine how thermal adaptation has changed due to climate change.

Colias (sulphur) butterflies range from lowland to alpine habitats across North America. *Colias eurytheme* is commonly known as the orange or alfalfa sulphur and is ubiquitious across North America below 2000m. *Colias eriphyle* occurs in open habitats

in the western US, and in western Colorado it is found at elevations of 1,400-2,900m. The larvae for both species feed on plants in the *Fabaceace* family, particularly *M. sativa* (alfalfa), *Vicia* (vetch) *spp., and Trifolium* (clover) *spp*. They have five larval instars and undergo a facultative diapause during the 3rd instar depending on local climate conditions. In my dissertation work I used these two species of *Colias* from four populations across the United States.

By using these species of *Colias* and the historical data available on local adaptation to temperature and host plants in larvae and plasticity in adults I am able to study changes local adaptation and plasticity over time. To do so in my dissertation I ask four major questions:

1. **Given the rate of climate change that has already occurred in the past 40 years, how has thermal local adaptation of *Colias* larval performance changed?**
2. **What are the long and short-term fitness effects of repeated exposure to sub-lethal high temperatures in *Colias eriphyle* larvae?**
3. **What are the effects of pupal temperature on pupal development and adult wing morphology in *Colias eriphyle?***
4. **What are the fitness effects of variable temperatures and the shift from a native host plant to an introduced host plant in Rocky Mountain *Colias eriphyle?***

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CHAPTER 2: GEOGRAPHIC DIFFERENCES AND MICROEVOLUTIONARY CHANGES IN THERMAL SENSITIVITY OF BUTTERFLY (*COLIAS)* LARVAE IN RESPONSE TO CLIMATE

Introduction

Populations are often adapted to the local climatic conditions that they experience, resulting in clines in many phenotypic traits along latitudinal and elevational gradients. Local adaptation over small spatial scales along elevational gradients has been documented in many taxa for a variety of phenotypic traits, including phenology (Hodkinson 2005), morphology (Roland 1978), body size, behavior (Dingle, Mousseau, and Scott 1990), thermal performance, and thermal tolerance (Stevens 1992, Badyaev and Ghalambor et al 2001, Damme et al. 1989, Gaston and Chown 1999).

Adaptation to climate is of increasing importance given the recent changes to regional and global climates, which are predicted to continue in the coming century (Easterling et al 2000, IPCC 2007). California, Colorado and other western states have shown a significant increase in the number of warm days and nights (where the maximum/minimum temperature is above the 90th percentile recorded from 1961-1990) since 1950 (Booth, Byrne, & Johnson 2012). The ecological consequences of recent climate change have been abundantly documented for many regions and taxa and include changes in seasonal timing, life history traits due to plasticity, geographic distribution and abundance, and extinction risks (Parmesan and Yohe 2003, Walther et al. 2002). In many cases, climate change is causing mismatches between local adaptation to past climates

and new climate conditions. A natural question is whether evolutionary responses to recent climate change can reduce this mismatch. Recent studies have documented evolutionary changes in response to climate change in body size or phenology in birds (Charmantier et al. 2008), mammals (Reale et al. 2003), mosquitoes (Bradshaw and Holzapfel 2001), alpine plants (Anderson et al 2012), and herbivorous insects (van Asch et al. 2013). Some contend that evolution in response to seasonal cues rather than thermal adaptation will be most important for evolutionary responses to climate change (Bradshaw and Holzapfel 2007, Karell et al. 2011). To date, evidence for evolutionary responses in thermal physiology to recent climate change has been limited (Stillman 2003, Huey, Patridge and Fowler 1991). Whether this is because such evolutionary changes are infrequent or unimportant or because there is a lack of appropriate historical data on physiological traits remains to be determined.

Colias butterflies have served as a model system for studying thermal adaptation for over 50 years (Ae 1958, Hoffman 1978). These butterflies range from lowland to alpine habitats across North America. Previous work, however, has largely focused on adult traits. In the Rocky Mountains of Colorado adult butterflies of *C. eriphyle* and closely related species demonstrate morphological adaptation to temperature in wing melanism and thorax fur thickness (Watt 1968, Kingsolver 1983a, Kingsolver 1983b). Little is known about *Colias* larvae and if they also display local adaptation to climate (Sherman and Watt 1973). Rates of larval feeding, growth, and development are essential to success, and are strongly temperature-dependent in most insects (Stamp and Casey 1993). The primary function of the larval life stage is to assimilate nutrients, and larvae do this by near-constant feeding. Sherman and Watt (1973) measured short-term rates of