BIOLOGY OF THE BAY CHECKERSPOT BUTTERFLY

We've been studying *Euphydryas* butterflies since 1960, when Paul Ehrlich started his work at Jasper Ridge. We started working in the East Hills (aka Kirby Canyon or Coyote Ridge) in the early 1980s, and have spent literally 1000s of person-days on site. Through the course of this work we've done a wide range of studies. I've taken a few summary paragraphs from some of our manuscripts, reports, proposals as background information for the WSSS field trip. **Alan Launer**

Habitat

The Bay checkerspot butterfly is restricted to patches of native California grassland containing a mixture of its larval hostplants (*Plantago erecta*, the primary larval hostplant, and *Orthocarpus densiflorus* or *O. purpurascens*, secondary larval hosts used when *Plantago* becomes senescent) and adult nectar sources (including *Lasthenia chrysostoma*, *Layia platyglossa*, *Allium* species, *Muilla maritima*, *Amsinkia intermedia*, and *Lomatium* species). This mixture of grassland forbs is regularly only found on serpentinitic soils. Serpentinitic rock weathers to form shallow, nutrient poor soils, typically low in nitrogen and calcium, and often high in magnesium, nickel, and chromium. Serpentinitic soils generally dry very rapidly, and as a result are exceedingly harsh environments for most plant species. For these reasons, grasses and forbs from Eurasia, which now dominate California grasslands on other soils, have been unable to do so on serpentinitic soils. As a result, the Bay checkerspot butterfly is currently restricted to remnant patches of native grasslands that are limited in area and isolated from one another.

Natural history

The Bay checkerspot butterfly is univoltine. Adults fly from late February to early May and females lay egg masses of up to 200 eggs at the bases of *Plantago* and *Orthocarpus*. Newly hatched larvae feed gregariously until oviposition plants are defoliated or senesce. Larvae that have not by then reached the appropriate size for diapause (an obligatory dormant period during the summer and autumn months when no food is available) must disperse and find additional hostplants. Only larvae that reach the fourth instar before the onset of the dry season are able to survive diapause. The single greatest source of natural mortality for Bay checkerspot butterflies occurs when larvae are unable to reach the appropriate size before the larval hostplants senesce.

Larvae remain dormant until the following rainy season when *Plantago* germinates. Postdiapause larvae feed from approximately December through February or early March. This is followed by a 10-20 day period as pupae. The precise timing and length of these life cycle stages is dependent upon local weather patterns. During periods of sunny weather, larvae rapidly develop. During cloudy and rainy periods, larvae cannot bask to raise their body temperatures and grow very slowly or not at all. Warm sunny winter weather, therefore, leads to earlier flight seasons than does cool rainy winter weather. The adult flight period may be three to five weeks in length, and can vary in onset from year to year from late-February to late-March. Individual butterflies typically live as adults for one to two weeks.

Variations in the timing of adult flight and hostplant senescence make Bay checkerspot butterfly populations highly prone to weather-induced population fluctuations. Following rainy seasons that favor prediapause larval survival -- many sunny days for postdiapause larval growth, but sufficient rainfall to keep plants growing late into spring -- the number of butterflies in a population may increase by a factor of five or more. During rainy seasons that provide dry conditions in the spring, larval hostplants senesce rapidly, prediapause survival may be extremely low, and the number of butterflies the following year may decrease by an order of magnitude. Not surprisingly, Bay checkerspot butterfly populations either declined or experienced local extinctions during the severe 1975-1977 drought. In addition, long periods of cloudy and rainy weather, such as during El Nino in 1982 and 1983, can delay larval growth and pupal development so that the adult flight season is late, lead to poor "phase relationship" with hostplant senescence. Population sizes decreased by an order of magnitude or more following that El Nino episode.

Topographic effects

The topographic configurations of individual patches of serpentine soil-based grasslands play a critical role in determining the ability of individual patches to sustain viable populations of the Bay checkerspot butterflies through extreme weather years. Variations in aspect and tilt angles across hillslopes provide distinct solar exposure regimes, which in turn create distinct microclimates. For example, south-facing slopes are warmer and drier than north-facing slopes, because south-facing slopes receive much more solar radiation on clear days than do north-facing slopes. This microclimatic variation affects the timing of both larval and hostplant development. Larvae on warm south-facing slopes may develop to adulthood a month (or more) earlier than larvae on cool north-facing slopes. Hostplant senescence is also dependent upon solar exposure; hostplants on south-facing slopes may flower and senesce three or four weeks before those on cooler slopes. The temporal phase relationship between adult flight and hostplant senescence, therefore, varies across the topography of the habitat.

The spatial pattern of prediapause survival across the microclimatic gradient changes from year to year. If the phase relationship between adult flight and hostplant senescence is favorable, prediapause larvae can survive on slopes warmer than those on which the preceding generation developed, and the population will experience a "thermal advance." Population increases are often associated with thermal advances. Conversely, if the phase relationship is poor, then prediapause larvae can only survive on slopes cooler than those on which the preceding generation developed, and the population will experience a "thermal retreat." Population declines are often accompanied by thermal retreats.

These ever-shifting patterns of larval survival emphasize the importance of topographic diversity in maintaining populations of the Bay checkerspot butterfly. Several topographic features contribute to long-term habitat quality. First is the overall range of slope exposures, which determines the overall range of microclimates. Relatively steep, north-facing slopes appear to serve as core habitat, because those slopes provide hostplants that remain edible for the longest period in the spring. Even small areas of cool north-facing slopes will confer to a population resistance to extinction during short or mild periods of drought. However, warmer slopes are also important. The lack of relatively warmer slopes adjacent to cool slopes will tend to retard postdiapause development, resulting in later flight periods and confounding the phase relationship between adult flight and hostplant senescence. A wide variety of microclimates across a patch of habitat assures that at least some survival, timely development, and reproduction can occur under most macroclimatic conditions. Even slopes with the very highest insolation, where the chances of prediapause survival are small, can contribute in some years by providing diverse early season nectar, which increases female fecundity and lifespan, and affects adult movement patterns.

The second topographic factor contributing to long-term habitat quality is the spatial interfacing between distinct microclimates. Areas with high local slope diversity are particularly valuable because postdiapause larvae can readily disperse from cooler to warmer slopes. Such movements can advance the emergence dates of those larvae by a week or more, increasing their chances of reproductive success.

Third, the amount of rainfall actually received by a site is important in determining soil moisture, which in turn determines the timing of hostplant senescence. The amount of rainfall varies widely over short distances in response to local rain shadows and elevation changes. Bay checkerspot butterfly populations residing in serpentine soil-based grasslands in higher rainfall zones are apparently more resistant to droughts, when any extra late season rainfall can make a significant contribution to extending the spring growing season.

Metapopulation dynamics

At the present time, it is thought that the Bay checkerspot butterfly exists in three metapopulations: one located in San Mateo County, one in south-central Santa Clara County, and one in the vicinity of Mt. Diablo. Each of these metapopulations consists of a dynamic mix of occupied and unoccupied habitat patches. Population extinctions and recolonizations are thought to be common occurrences in each metapopulation. While, dispersal between the three metapopulations is minimal, dispersal between close habitat patches within a metapopulation is fairly common. However, dispersal farther than five kilometers is relatively uncommon and 95% of all dispersal events documented through nearly 40 years of research have been less than 500 meters. It should be noted that at least three populations in the Santa Clara County metapopulation frequently consist of more than 250,000 adult butterflies, meaning that at a population level, large numbers of butterflies occasionally disperse comparatively long distances.

Additional and on-going studies

Long-term monitoring and status of regional populations of the Bay checkerspot butterfly. We conduct in depth monitoring of the number and distribution of Bay checkerspot butterflies at several locations and visit virtually all known habitat patches in the area on a rotating basis.

Distribution of plants and moths. We have been working the last five years to determine the spatial distribution of plants and moths at Kirby Canyon. Field data have been entered into our computer databases, analyzed, processed, and graphed back onto our GIS-based landscapes. We also have expanded these studies to other sites in the region.

Impacts of nitrogen deposition on serpentine grasslands. Even though serpentine-based soils act to exclude non-native plant species, this exclusion is far from complete. Throughout Santa Clara County serpentine grasslands that are not either grazed or subject to wildfires are invaded by non-native grasses. These invasions are apparently being made much worse by nitrogen deposition -- with the source of nitrogen being air pollution. Preliminary work by Stu Weiss indicates that this deposition is perhaps a major problem for the local serpentine grasslands (similar air pollution-related deposition has been shown to be a problem in other nutrient-poor systems).

GIS modeling of the serpentine grassland ecosystem. We have constructed a variety of GIS-based models in order to further analyze the serpentine grasslands of the Bay Area. While our primary focus has been on the Coyote Valley region, we have expanded our coverage to include the San Mateo sites as well.

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Note: *Orthocarpus densiflorus* and *O. purpurascens* are now designated *Castlleja densiflora* and *C. exerta* (J.C. Hickman, editor, 1993, *The Jepson Manual*)

Alan E. Launer, Ph.D.
Center For Conservation Biology
Department of Biological Sciences
Stanford University, Stanford CA 94305-5020

(650) 725-1854
fax (650) 723-6150

aelauner@leland.stanford.edu

Jasper Ridge Serpentine Grassland tour

Jasper Ridge Biological Preserve of Stanford University is a 489 ha protected area on the extreme western end of campus. The roughly diamond-shaped Preserve is located on the eastern flank of the Santa Cruz Mountains and slightly overlaps the San Andreas Fault zone and several lesser faults. The eponymous ridge extends from the southeast to northwest of JRBP and is obliquely bisected by a jagged, discontinuous band of serpentine grassland totaling about 20 ha, with an additional 5 ha of serpentine chaparral on the western flank of the grassland. On either side of the serpentine grassland are grasslands on different substrates. The serpentine grassland supports a diverse community of native grasses and forbs (roughly 100 species) and generally excludes invasive Eurasian species that have outcompeted native species on other substrates. The area is a refugium both for native plants and for animals that depend on them, such as the threatened *Euphydryas editha bayensis*.

JRBP has been part of Stanford University for more than a century, and is open to researchers from any institution to conduct approved studies. This tour will visit an area of serpentine grassland where various longterm ecological studies have occurred, including studies of the threatened Bay Checkerspot butterfly, the effects of gophers on plant community composition, plant population genetics and ecotypic variation, seed-harvesting ants, responses of grassland to increased atmospheric carbon dioxide, and other studies. Several of these studies are briefly summarized below.

Longterm studies of the Bay Checkerspot butterfly

Studies of *Euphydryas editha bayensis*, or Bay Checkerspot butterfly, were started by Professor Paul Ehrlich in 1960 and have examined many aspects of the ecology and population biology of this butterfly, which was federally listed in 1987 as a "threatened species". Studies have included mark-release-recapture studies of population size and sex ratio; larval feeding ecology; reproductive behavior; isozyme analysis of genetic differentiation; gene flow within the Preserve and between the Preserve and other sites; microclimate effects on mortality; predation; nectaring behavior; protandry; and hilltopping. We will visit the largest of the serpentine grassland "islands" where studies of *Euphydryas editha* have been conducted. In recent years, the butterfly has been extinct in this and a second site, while a third site has had small and declining populations of adults.

Longterm studies of gopher exclusion and rainfall variability

Since 1982, Richard Hobbs (CSIRO, Australia) and Harold Mooney (Stanford University) have monitored experimental plots within the serpentine grassland, some of which have hardware cloth barriers to exclude gophers. They have mapped plant community composition and gopher disturbance annually. During their study they have found that most of the area is disturbed at least once every 3-5 years by gophers. Gopher disturbance level was not related to rainfall (which ranged from 200-1200 mm per year) but the patterning of disturbance was related to soil depth. Following establishment of exclosures, perennial species increased in abundance and then later declined. Data on plant densities on gopher mounds disturbed at different times of year and in different years indicate that local species composition remains distinct for a number of years following disturbance.

Studies of population genetics and ecotypic variation

Several current studies examine differentiation within plant populations occurring on serpentine substrates and as well as differentiation between populations occurring on serpentine and non-serpentine substrates. Prof. Bruce Bohm (Univ. British Columbia) has conducted longterm studies of a common serpentine grassland forb, *Lasthenia californica*. We will visit the sites where he has identified a consistent pattern of distribution of two subpopulations that can be distinguished by pappus shape, isozymes and flavonoid chemistry. Regional studies have found that these types represent geographical races, which apparently co-occur only at Jasper Ridge. Other studies by his group are looking at soil chemistry in the areas occupied by the two races.

Another species, *Linanthus parviflorus*, shows an association between flower color and soil type: flowers are almost always pink on serpentine and predominantly white on sandstone substrates. We will visit field sites where Prof. Douglas Schemske (Univ. Washington) is investigating the genetic basis of this pattern and how it is maintained. He has studied a very similar flower color "polymorphism" in *Linanthus parryae* in the Mojave Desert. Breeding studies with plants grown from Jasper Ridge seed have shown that pink is dominant to white in the determination of flower color. Schemske is also testing whether flower color is linked with other traits that improve survival or reproduction on the different types of soil; in particular he is interested in whether flower color is associated with the more rapid drying of serpentine soils (as compared with sandstone), which might select for earlier flowering and/or ability to tolerate low soil moisture.

Seed harvesting ants

The harvester ant *Messor andrei* is a major seed predator on serpentine grassland, especially for some highly preferred seed species such as *Microseris douglassii*. Seeds of less preferred species, such as the dominant annual species, *Lasthenia californica*, are not foraged until later in the summer when seeds of other species are less abundant. We will visit areas of serpentine grassland where nest densities of *Messor andrei* are roughly 70 per ha, and the ants have a significant effect on plant community structure. Recent studies by Mark Brown (Stanford University) have detailed the foraging behavior and nest re-location dynamics of this species.

Grassland response to global change

A recently completed study directed by Christopher Field (Carnegie Institution) and Harold Mooney (Stanford University) examined the roles of resource availability, species characteristics, and community composition in controlling ecosystem responses to increased CO_2. The serpentine grassland that we will visit, together with adjacent grassland on sandstone soils, provided a comparative system for looking at the response of natural grasslands, differing in productivity, to a doubling of atmospheric CO_2. The study found that most plant responses to CO_2, such as increased plant growth, are consistently greater when nutrients are less limiting. Most of the growth increase under high CO_2 is due to increased water-use-efficiency and soil moisture under elevated CO_2. Improved soil moisture under high CO_2 also tends to extend the growing season, which favors species with longer or flexible lifespans, such as tarweeds.

Western Society of Soil Science

field trip

San Francisco, California

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Field Trip Stops and Points of Interest (v) Located on the Map:

- 0 - SFSU, San Francisco State University
- 1 - HPS, Hunters Point Shipyard
- v - Communication Hill
- 2 - Coyote Ridge, at Kirby Canyon Recycling and Disposal Facility
- 3 - Jasper Ridge, at Jasper Ridge Biological Preserve
- v - CSD, Crystal Springs Dam