OVIPOSITION PREFERENCE IN TAYLOR'S CHECKERSPOT BUTTERFLIES (*EUPHYDRYAS EDITHA TAYLORI*): COLLABORATIVE RESEARCH AND CONSERVATION WITH INCARCERATED WOMEN

by

Dennis Aubrey

A Thesis
Submitted in partial fulfillment
of the requirements for the degree
Master of Environmental Studies
The Evergreen State College
June 2013

This Thesis for the Master of Environmental Studies Degree

by

Dennis Aubrey

has been approved for

The Evergreen State College

By

Carri J. LeRoy
Member of the Faculty

Date

ABSTRACT

Oviposition preference in Taylor's checkerspot butterflies (*Euphydryas editha taylori*): Collaborative research and conservation with incarcerated women

Dennis Aubrey

Taylor's checkerspot butterfly (*Euphydryas editha taylori*) is a federally threatened pollinator of increasingly rare prairies in the Willamette Valley-Puget Tough-Georgia Basin ecoregion. Since the arrival of European settlers, land use changes, habitat fragmentation, and invasive species have contributed to a decline in available native host plants for *E. e. taylori* larvae. The most commonly utilized host is now lance-leaf plantain (*Plantago lanceolata*), an exotic species long prevalent in the area. None of the known native hosts are ideal for supporting *E. e. taylori* recovery efforts, so *P. lanceolata* is currently planted at butterfly reintroduction sites. Golden paintbrush (*Castilleja levisecta*), a federally threatened perennial, does not now co-occur with *E. e. taylori* but may have been an important host historically and could be more suitable than the known native hosts. Previous work has shown that oviposition preference is: 1) heritable and may provide clues as to which hosts were historically important, and 2) is correlated with larval success so might indicate which native hosts would be most effective at restoration sites. I undertook a manipulative oviposition preference experiment to determine which potential hosts were preferred by *E. e. taylori* among *P. lanceolata*, *C. levisecta*, and harsh paintbrush (*Castilleja hispida*), a known native host. The two *Castilleja* spp. were preferred equally, but both were preferred over *P. lanceolata*. If further research confirms the suitability of *C. levisecta* as a host for *E. e. taylori*, restoration efforts for the two species could be united, and the effectiveness of both might be synergistically increased. This project was undertaken collaboratively with inmates at Mission Creek Corrections Center for Women with support from the Sustainability in Prisons Project and the Washington Department of Fish and Wildlife, and seeks to benefit multiple stakeholders through an interdisciplinary intersection of conservation biology and social sustainability.

TABLE OF CONTENTS

LIST OF FIGURES

ACKNOWLEDGEMENTS

The butterfly facility at Mission Creek Corrections Center for Women is managed by the Sustainability in Prisons Project and Washington Department of Corrections staff, overseen by the Washington Department of Fish and Wildlife, assisted by the endangered butterfly lab at the Oregon Zoo (Portland, Oregon), and funded by a US Fish and Wildlife Grant through the US Army Compatible Use Buffer program. I thank all of these partners, The Evergreen State College, and WDOC administration for their support of both this research and the overarching vision of bringing science and nature into prisons. I also thank the individuals that made this research a reality: biologist Mary Linders from WDFW; Kelli Bush, Joslyn Trivett, and Carl Elliott from SPP; undergraduate interns Caitlin Fate and Chelsea Oldenburg from TESC; Superintendent Wanda McRae, Anne Shoemaker, Leo Gleason, Sherri Albrecht, and Dan Davis from MCCCW; Ted Thomas of the U.S. Fish and Wildlife Service; Mary Jo Andersen and Karen Lewis from the Oregon Zoo; and five inmates, who will remain unnamed, that supported and participated in gathering these data. Lastly, my reader Carri LeRoy provided tireless guidance on everything from methods design to statistical analysis and preparation for peer-reviewed publication.

INTRODUCTION & LITERATURE REVIEW

The prairies and oak savannas of the Willamette Valley-Puget Sound-Georgia Basin (WPG) ecoregion, in the western United States, are increasingly rare and are recognized as one of the most endangered ecosystem types in the region (Noss et al. 1995, Floberg et al. 2004, Stanley et al. 2008, Dunwiddie and Bakker 2011). Early descriptions of the vegetation and habitat types within the WPG come from David Douglas who explored the area in the early 1800's. Then Lang (1961) briefly described the prairies of the south Puget lowlands, a subregion of the WPG, as being a mosaic of grasslands, oak and conifer savannas, and wetlands. The first overview of WPG prairies was provided by Franklin and Dyrness (1973), but more detailed surveys were still needed. Giles (1970) and del Moral and Deardoff (1976) surveyed small subsets of regional prairies but not until Chappel and Crawford (1997) was the vegetation exhaustively catalogued. These 1997 surveys provide a valuable baseline for current and future analyses of changing plant ranges and assemblages.

Today, one of the defining characteristics of WPG prairies is their scarcity. In the south Puget lowlands, high quality prairie cover has declined to 3% of its historic extent based on soil surveys (Crawford and Hall 1997); however, if semi-native and non-native grasslands are included, 24.4% remain (Figures 1 & 2). The first to note the spatial decline of the grassland/woodlands in the region was Giles (1970), who examined Douglas-fir (*Pseudotsuga menzesii* (Mirb.) Franco) encroachment on south Puget lowland prairies. Further studies

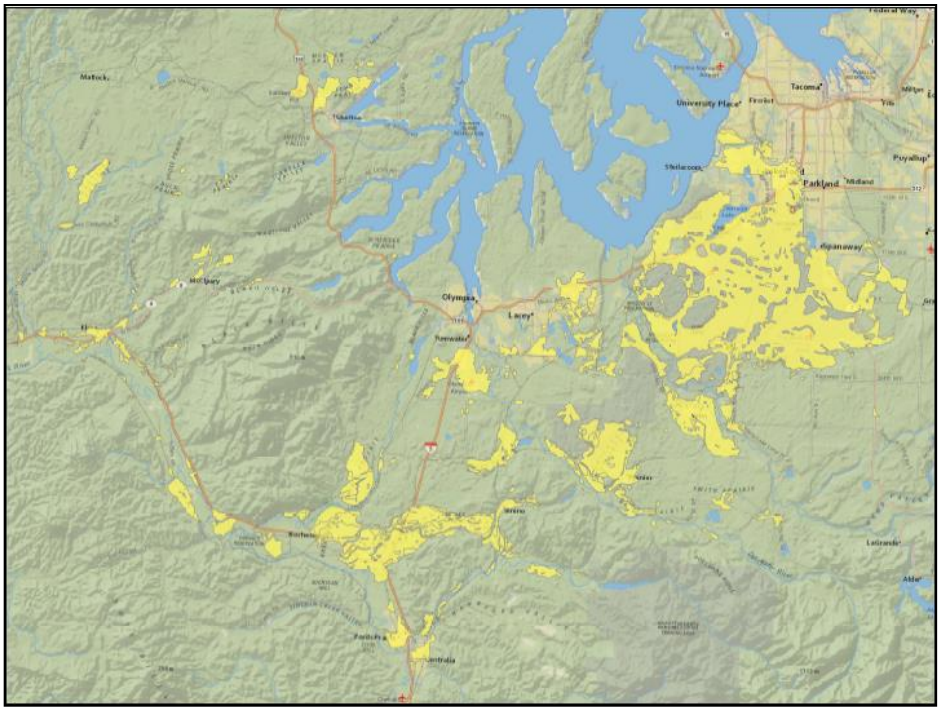

Figure 1. Historic prairies (based on soil surveys), in the south Puget lowland ecoregion: 173,261 acres; largest patch: 63,641 acres; mean patch size: 262 acres; adapted from Crawford et al. 1994

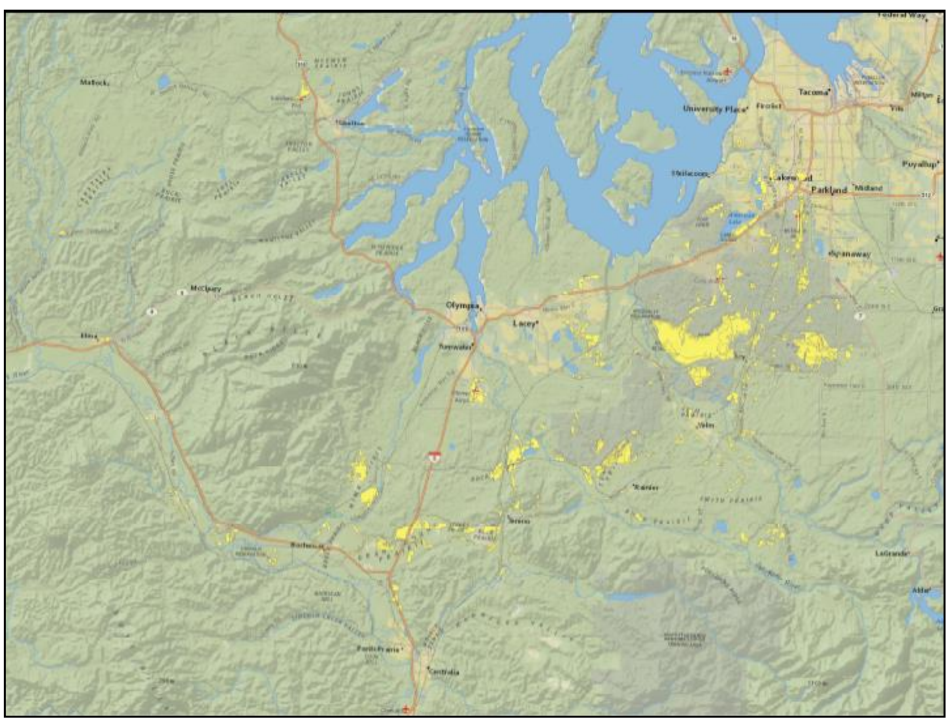

Figure 2. Remaining grasslands and prairies (2005): 42,353 acres (24.4%); largest patch: 3,778 acres (5.9%); mean patch size: 18 acres (6.9%); adapted from Crawford and Hall 1997

surveyed the flora of these ecosystems in natural (del Moral and Deardorff 1976) and disturbed (Jackson 1982) settings, but it was not until Clampitt (1993) that the differences between natural and disturbed Puget lowland prairies were quantified. Clampitt (1993) concluded that no native prairies remain in western Washington, and that at least one native species (*Aster curtis*) was unable to persist in disturbed habitats. More projects followed these, and it is now clear that land use changes, habitat fragmentation and invasion by exotics have all contributed to the continuing decline in both the extent and functionality of these prairie ecosystems (Fimbel 2004, Grosboll 2004, Stanley et al. 2008), and many obligate species have become imperiled as a result (Dennehy et al. 2011, Hamman et al. 2011, Schultz et al. 2011, Wold et al. 2011).

One important concern for situations involving multiple declining species involves the potential of lost interactions. For example, Kearns et al. (1998) explored “endangered mutualisms” with respect to loss of pollination services. Particularly, they discuss the effects of population decline and habitat fragmentation in decreasing the pollinator/host interactions among declining species, and argue that such impacts could range in severity according to the dependence of the interaction. This was one of the earliest times this concept had been discussed in a community ecology context, and it opened the door to a growing body of work on the topic of co-extinction (Koh et al. 2004, 2004, Rezende et al. 2007, Dunn et al. 2009). Further work modeling the effects of lost mutualisms across phylogenetic trees was done by Rezende (2007), showing that co-extinction leads to “non-random pruning” of phylogenetic tree branches. Pin

Koh et al. (2004) modeled other species relationships at risk of facilitating co-extinction, including parasites and their hosts such as butterflies and their larval host plants, and concluded that 6300 known species were “co-endangered” because of an interaction with another listed species. Dunn et al. (2009) summarized that the two broad interactions most likely to facilitate co-extinction are mutualism and parasitism, due to the highly specific dependence often associated with these relationships.

Two threatened species found on WPG prairies, the ranges of which were broadly overlapping historically but do not now co-occur, are Taylor’s checkerspot butterfly (*Euphydryas editha taylori*), and golden paintbrush (*Castilleja levisecta*). Possible historic interactions between these two species would certainly have included mutualistic pollination, but if it could be shown that *E. e. taylori* utilizes *C. levisecta* as a larval host, it could also have included parasitism. If we accept the premise that mutualism and parasitism are separately the two most dangerous interactions for declining species in terms of co-extinction risk (Dunn et al. 2009), we can conclude that the continued isolation of *E. e. taylori* and *C. levisecta* is a particularly urgent conservation concern.

TAYLOR’S CHECKERSPOT BUTTERFLY

Euphydryas editha taylori is a non-migratory butterfly species, federally listed as potentially endangered (2012), which once flourished on glacial outwash prairies, low elevation grassy balds and coastal grassland sites from southern British Columbia to central Oregon (Grosboll 2004, Schultz et al. 2011, Severns and

Grosboll 2011). The species was first named by W. H. Edwards in 1888 after Reverend George W. Taylor, one of the first lepidopterists to work in British Columbia (Shepard and Guppy 2011). Gunder (1929) thereafter described two other subspecies (*E. e. barnesi*, and *E. e. victoriae*) that are now considered synonymous with *E. e. taylori*. Phenotypically, *E. e. taylori* is the darkest *editha* subspecies. It has black wings brightly checkered with orange and white spots, and an average wing span of ca. 4 cm, making *E. e. taylori* one of the smallest *editha* subspecies.

<u>Species status, life history, and restoration challenges</u>

Taylor's checkerspots were relatively abundant until fairly recently, according to Pyle (1974) and Dornfield (1980) who said that in western Oregon before 1970 they were known to "swarm by the thousands." Since 1970, factors such as land use change, habitat fragmentation, and invasion of remnant prairies by exotic shrubs and grasses all combined to reduce populations of *E. e. taylori* to the point that they were thought to be extinct (Pyle 2002, Severns and Warren 2008). It was not until they were rediscovered by a junior author during the preparation of *The Butterflies of Cascadia* (Pyle 2002) that conservation efforts began. Since then, efforts to quantify the status of the species (Shepard 2000, Ross 2003, Black and Vaughan 2005, Stinson 2005) have led to the conclusion that eight known populations of *E. e. taylori* continue to persist (Schultz et al. 2011).

Before its decline, *E. e. taylori* had not been intensively studied, so initial hypotheses of *E. e. taylori* habitat needs and host plant interactions were augmented by cautious inference from research done with other *E. editha* subspecies. Fortunately, these are some of the most studied butterflies in North America (Ehrlich and Hanski 2004). For example, work by Weiss, Murphy, and White (1988) had shown that topographic diversity, and its associated microclimatic heterogeneity, was an important determinant of habitat quality for California populations of bay checkerspots (*E. e. bayensis*). This conclusion was drawn from several observations. First, on warmer slopes, post-diapause larvae pupated earlier and pupa developed to eclosion more rapidly than on progressively cooler slopes. Furthermore, females which eclosed earlier were more reproductively successful because egg clutches laid earlier tended to be more successful on a wider variety of slopes than those laid comparatively later. This was because larval host plants on the sunnier slopes began to senesce in the latter part of the season, which caused significant mortality in pre-diapause larvae. Therefore, warmer slopes were advantageous for post-diapause larvae and adults, but eggs and pre-diapause larvae showed better survivorship on cooler slopes (Weiss et al. 1988).

Other insights gleaned from previous *E. editha* research related to dispersal traits and metapopulation dynamics. Early work by Ehrlich (1961) had shown that *E. editha* was similar to other butterflies in that, despite the high potential vagility (ability to disperse across barriers) associated with flight, their populations tended to remain fairly sedentary. This understanding about the difference between potential and actual vagility in *E. editha*, and the implications of low actual vagility on gene flow within metapopulations and the species' ability to colonize new sites (or recolonize old ones), led to a four year study of a single metapopulation at Jasper Ridge, California (Ehrlich 1965). This study showed that very little gene flow occurred between populations even when there was no discernible habitat discontinuity separating them. Furthermore, populations tended to shift spatially very little and did not expand to take advantage of unutilized resources at the fringe. Later work showed that populations were subject to relatively frequent extirpations (Ehrlich et al. 1980) but that the few colonizations of new sites which did occur (Singer and Ehrlich 1979) served to offset this, resulting in a metapopulation which persisted as a shifting mosaic of relatively isolated subpopulations (Singer and Ehrlich 1979, Harrison et al. 1988). Singer and Ehrlich (1979) warned of the potential impact of any factor which decreased the rate at which new sites were successfully colonized. In light of this previous research on related species, the need for relatively large contiguous habitat patches could be especially problematic for *E. e. taylori* which exists in a highly fragmented landscape (Char and Boersma 1995, Dunwiddie and Bakker 2011, Schultz et al. 2011).

Another threat to the continued persistence of *E. e. taylori* is posed by a shift in plant assemblage on remaining prairies, from native forbs and bunch grasses to invasive shrubs, forbs, and tall grasses (Stanley et al. 2008, Dunwiddie and Bakker 2011). This shift may inhibit the ability of *E. e. taylori* to colonize new sites and so reduce the functionality of metapopulations. Tall grasses in particular may be harmful to *E. e. taylori* persistence (Weiss 1999, Severns and Warren 2008). Weiss (1999) showed that California populations of *E. e. bayensis* tended to persist in areas dominated by native grasses, but often crashed shortly after invasion by taller exotic species. Severns and Warren (2008) showed that gravid *E. e. taylori* females chose sites for oviposition that were surrounded by a higher abundance of native plants and short grasses, as opposed to taller exotics.

In many cases invasion of prairies by exotic plants causes the remaining natives (if any remain) to persist only on less suitable, more xeric soils (Fimbel 2004), a fact which may exacerbate the effects of invasive plants on *E. e. taylori* populations. Even a small shift towards earlier senescence by *E. e. taylori*'s native host plants could reduce larval survival, since a major source of mortality for *E. editha* larvae is premature host plant senescence (Ehrlich 1961, Mackay 1985, Grosboll 2011). Even a shift of a single week could mean the difference between larvae successfully entering diapause or dying in the sun on a desiccated host plant.

Anticipated effects of regional climate change

Another potential influence on *E. e. taylori* populations, which may be increasingly severe in the future, is posed by regional climate change. In a study of two extirpations of *E. e. bayensis* in California, McLaughlin et al. (2002) found that their population declines were more precipitous as a result of increased variability in precipitation. Global and regional climate models predict that precipitation variability in the Pacific Northwest will increase (Solomon et al. 2007). McLaughlin et al. (2002) also modeled extant populations of *E. e. bayensis* to examine the influences of such a trend, and found that increased precipitation variability caused populations to fluctuate dramatically leading to swift extinctions, especially when coupled with increased fragmentation of habitat.

Current regional climate models predict a general warming throughout the WPG of 1.1 °C by the 2020's and 3.0 °C by the 2080's (Mote and Salathé 2010). Precipitation variability is expected to increase, with more winter rainfall but prolonged summer droughts (Mote and Salathé 2010, Bachelet et al. 2011). The frequency of extreme weather events is also expected to increase. Potential effects of these changes to *E. e. taylori* have not been specifically studied, but could include increased population variability (McLaughlin et al. 2002), temporal shifts in life stages or changes in diapause length, or increased mortality from anomalous weather events.

In addition to direct effects of climate change on *E. e. taylori*, indirect effects may also exist from changes to habitat characteristics and host/nectar plant availability. The effects of regional climate change on WPG prairies have been predicted by effect simulations and warming experiments. Effect simulations have been focused primarily on trees, and predict a range shift by *P. menzesii* northward (Hamann and Wang 2006) and upward (Rehfeldt et al. 2006, Coops and Waring 2011). Because of this, it is anticipated that forest encroachment on lowland WPG prairies will be reduced (Bachelet et al. 2001, Shafer et al. 2001, Rehfeldt et al. 2006, Littell et al. 2010, Coops and Waring 2011) except in the northernmost parts of the ecoregion (Hamann and Wang 2006). In grassland sites across the globe, several warming experiments have shown an overall decline in plant biodiversity (Zavaleta et al. 2003, Klein et al. 2004, Walker et al. 2006), which corroborates the prediction of decreased competition from *P. menzesii*, and also goes a step further and predicts species loss across a wider range of taxa. Still, plants native to WPG prairies are well adapted to summer droughts and nutrient-poor soils. Fimbel (2004) found that natives were often able to persist in marginal conditions unsuitable for exotics, and Pfeifer-Meister et al. (2008) found that native vs. exotic success was controlled by moisture and nutrient availability. Therefore, there is the potential that the loss of biodiversity associated with a warming climate might favor native plants. Complicating the picture, however, are other experiments that found the negative effects associated with warming were offset by increases in nutrient availability which might favor invasives (Shaver et al. 2000, Rustad et al. 2001, de Valpine and Harte 2001, An et al. 2005, Suttle et al. 2007). Because of these contrasting factors, a summative prediction of climate change impacts to WPG prairies is difficult to make (Bachelet et al. 2011), but even small changes to host plant availability could have dramatic effects on *E. e. taylori* populations.

Habitat restoration

Facing the multitude of challenges listed above, conservation efforts for *E. e. taylori* have been underway for over a decade. These efforts have focused on conservation of existing populations (primarily through invasive plant removal), restoration of habitat for reintroduction, translocation, and captive breeding.

The restoration of habitat for *E. e. taylori* has been informed by several studies. Hays et al. (2000) conducted an extensive survey of two south Puget lowland prairies (Scatter Creek Wildlife Area and Johnson Prairie on Joint-Base Lewis McChord) to assess habitat characteristics and plant usage by *E. e. taylori*. This study provided an early baseline for restoration targets at sites being prepared for translocation of the butterflies. Previous studies with related species also help inform *E. e. taylori* restoration decisions, such as Ehrlich and Murphy (1987) who reviewed conservation lessons learned from several long-term studies with *E. editha* spp. and provided insight on supplying resources for all life stages in the design of restoration projects. Another study, which informs our understanding of *E. e. taylori*'s ideal habitat characteristics, was provided by Singer (1972) who showed that gopher mounds provided enough microclimatic variation to increase larval survival in *E. e. bayensis*. Larval host plants growing on the mounds resisted summer drought longer than those growing in the intermound space, and provided a mechanism for larval survival in dry years. These findings may be relevant for *E. e. taylori* because Mazama pocket gophers (*Thomomys mazama*) historically occupied a similar range of Puget lowland prairies, and currently co-exist with *E. e. taylori* in the location of its largest extant population. Mazama pocket gophers are also candidates for listing under the Endangered Species Act.

Another important habitat characteristic which *E. e. taylori* has adapted to is the presence of fire. Western Washington prairies were burned by Native Americans nearly every year, for about 15,000 years, prior to the arrival of European settlers in the middle of the 19th century (Morris 1934, Lang 1961, Norton 1979, Leopold and Boyd 1999, Fimbel 2004, Storm and Shebitz 2006).

Humans burned prairies annually in many locations to increase the availability of edible forbs, and every few years in other places to increase the abundance of berries (Norton 1979, Fimbel 2004, Storm and Shebitz 2006). This adaptation of *E. e. taylori* to fire-altered habitats may be partly responsible for the unusual location of its largest extant population: the Artillery Impact Area (AIA) at Joint Base Lewis-McChord (Linders 2012). Fires still burn the prairie nearly every summer on the AIA, set by practice shelling with explosive ordinance (Tveten 1997). Other factors which may also contribute to *E. e. taylori* persistence at this site include the sheer size (> 3000 ha) of the habitat fragment (MacArthur 1967, Quammen 2012), as well as the presence of Mazama pocket gophers (Stinson 2005). Also, the restriction against development and recreational use of military lands may reduce other negative human influences on *E. e. taylori* populations.

Endangered butterflies living on a valuable army training asset is a strangely beneficial relationship for *E. e. taylori* recovery efforts. Department of Defense biologists are tasked with species conservation and restoration on federal lands. A dedicated staff of these biologists and ecologists is employed at JBLM and is actively engaged in on-site restoration on a year-round basis. Furthermore, a grant program, called the Army Compatible Use Buffer (ACUB) program, focuses on purchasing and restoring non-military land in the vicinity of military bases. One of the stated purposes of the ACUB program is reducing the negative influences of training activities on imperiled species, and it has been instrumental in supporting *E. e. taylori* captive rearing and translocation efforts in the south Puget lowlands (Linders 2012).

Translocation and captive breeding

When recovery efforts began for *E. e. taylori*, there were two populations that were considered robust enough to serve as sources of individuals for captive breeding and translocation. These were the AIA at JBLM as mentioned above and another site in western Washington, a series of grassy knolls called the Bald Hills (Linders 2007). The Bald Hills population is now considered extirpated (Grosboll 2011) leaving only one source population range-wide.

Nine unoccupied sites were initially considered as potential restoration areas for experimentally reintroducing *E. e. taylori* (Linders 2007). These included sites both on and off the JBLM military base. To date, *E. e. taylori* releases have occurred at four sites (Linders 2012): Scatter Creek Wildlife Area (since 2007), Range 50 on the AIA at JBLM (2009-2011), Pacemaker on 13th Division Prairie at JBLM (2012), and Glacial Heritage Preserve (since 2012).

Because of the need for an increasing number of animals for release, and the uncertainty of the source population, effort has also been focused on the development of captive breeding methods (Grosboll 2004, Linders 2007, 2012, Barclay et al. 2009). Captive breeding began with a pilot project by Grosboll (2004) who attempted to rear 126 eggs collected from a wild female using two different host plants, lance-leaf plantain (*Plantago lanceolata* L.) and harsh paintbrush (*Castilleja hispida* Benth.). His results showed no difference from hatching to diapause, but better survival from diapause to eclosion for the *C. hispida* group. Efforts were moved to the Oregon Zoo in 2004, where a successful standardized protocol has been developed (Barclay et al. 2009). A second captive breeding institution was added to the project in 2012, in association with the Sustainability in Prisons Project, at Mission Creek Corrections Center for Women. This facility was able to build on the work accomplished by the Oregon Zoo in achieving a 96.6% egg to diapause survivorship in their first year of operation. With both facilities operating successfully, the largest release to date was held in 2013, when over 6000 animals were released at Scatter Creek Wildlife Area and Glacial Heritage Preserve.

Oviposition host plants

Ecological restoration to prepare sites for reintroduction of *E. e. taylori* is underway, but conservation planners are uncertain which plants were historically the butterfly's most important larval hosts (Severns and Warren 2008). At present, *E. e. taylori* primarily utilizes the introduced exotic, *P. lanceolata* for oviposition. One reason for this is that *E. e. taylori* utilizes an unpalatability defense, by ovipositing selectively on plants which contain iridoid glycosides (Grosboll 2004, Schultz et al. 2011). Upon hatching, the larvae consume these monoterpenes, sequestering them in their tissues and ultimately discouraging predation throughout their life cycle (Bowers 1981). *Plantago lanceolata* contains iridoid glycosides, as do the other native plants *E. e. taylori* is known to oviposit on, such as *C. hispida*, shortspur seablush (*Plectritis congesta* (Lindl.) D.C.), and maiden blue-eyed Mary (*Collinsia parviflora* Lindl.). Despite having suitable native hosts, however, *E. e. taylori* has come to be almost completely dependent on *P.*

lanceolata due its spatial density and abundance, and the decreasing abundance of the native species (Severns and Warren 2008).

The fact that *E. e. taylori* has switched hosts to a potentially invasive exotic plant presents a problem for restoration management. The idea of introducing a noxious weed to otherwise high quality native prairie is unpopular, but other options are few. The native plants known to be occasional larval hosts to *E. e. taylori* typically senesce on WPG prairies before the larvae are able to successfully enter diapause (Mary Linders, personal communication). In contrast to the natives, *P. lanceolata* tolerates drought quite well and often persists throughout the summer.

GOLDEN PAINTBRUSH

One native plant which shows promise as a larval host is another federally-threatened species, golden paintbrush (*Castilleja levisecta* Greenm.). This iridoid glycoside-producing perennial shares with *E. e. taylori* approximate historic range (Wentworth 2001, Lawrence and Kaye 2008, 2011), preferred habitat type, and reasons for population decline.

Castilleja levisecta was first collected in 1875 in Victoria, B.C., and was first described by J. N. Greenman in 1898. Historically, it has been collected from over 30 sites, but by 1981 it had declined in abundance and was listed on the first publication of the Washington Natural Heritage Program's list of endangered species. Field surveys by Sheehan and Sprague (1984) and Evans, Schuller, and Augenstein (1984) quantified how rare it had become, which led to its 1997 federal threatened-species listing. Following this, Wentworth (1994) further studied the phenology and life history traits of *C. levisecta*. Unfortunately, the species was already extirpated from most of its range before Wentworth did his research, so the true variability of its phenology and preferred habitat characteristics have been difficult to estimate (Gammon 1995, Lawrence and Kaye 2006).

Currently, there are 11 isolated populations of *C. levisecta*, ten of which are in the San Juan Islands and British Columbia (Lawrence and Kaye 2008, 2011). Additionally, there are no co-occurring populations of *C. levisecta* and *E. e. taylori*. Because of this, it is unknown if *E. e. taylori* will oviposit on *C. levisecta*, but it is recognized that in several ways it might be highly suitable. For example, *C. levisecta* occupies slightly more hydric microsites than the known native hosts and it often persists well into the summer months (Wentworth 2001). Additionally, its growth form may provide more available biomass for larval consumption than *C. hispida*, so it might be able to host larger populations per plant. These lines of evidence, combined with the fact that the timing of the two species' decline has been relatively coincident, have led to speculation that *C. levisecta* could be an ancestral host for *E. e. taylori* (Stinson 2005).

Despite the apparent suitability *C. levisecta* as a larval host, it has not been experimentally reintroduced to *E. e. taylori* habitat sites because congeneric *C. hispida* is actively planted and the two could hybridize if grown together (Lawrence and Kaye 2008). Research is currently ongoing to address the question of *Castilleja* spp. hybridization rates, but until this is known the only option would be to replace *C. hispida* with *C. levisecta* at restoration sites, and that represents too much of a risk without verification of the suitability of *C. levisecta* as a host plant. However, *C. levisecta* is currently reintroduced at separate restoration sites, and if it could be shown that *E. e. taylori* will select it for oviposition, the two restoration efforts might be joined. This has the potential to increase the effectiveness of both *C. levisecta* and *E. e. taylori* recovery efforts, and is the subject of this thesis.

ARTICLE MANUSCRIPT

Formatted for submission to Northwest Science

Oviposition preference by Taylor's checkerspot butterfly (*Euphydryas editha taylori*) among lance-leaf plantain (*Plantago lanceolata*), harsh paintbrush (*Castilleja hispida*), and golden paintbrush (*Castilleja levisecta*)

ABSTRACT

Taylor's checkerspot butterfly (*Euphydryas editha taylori*) is a federally threatened pollinator of increasingly rare prairies in the Willamette Valley-Puget Trough-Georgia Basin ecoregion. Since the arrival of European settlers, several factors have helped reduce available native host plants for *E. e. taylori* larvae. The most common host is now *Plantago lanceolata*, an exotic species long prevalent in the area. None of the known native hosts are ideal for supporting *E. e. taylori* restoration. Federally threatened *Castilleja levisecta* may have been important historically but does not now co-occur with *E. e. taylori*. Previous work has shown that oviposition preference is: 1) heritable and may provide clues to which hosts were historically important, and 2) correlated with larval success so might indicate which hosts would be most effective for restoration. We undertook an oviposition preference experiment to determine which potential hosts were preferred by *E. e. taylori* among *P. lanceolata*, *C. levisecta*, and *C. hispida*. The two *Castilleja* spp. were preferred equally and both were preferred over *P. lanceolata*. If further research confirms the suitability of *C. levisecta* as a host for *E. e. taylori*, restoration efforts for the two species could be united, and the effectiveness of both might be synergistically increased.

INTRODUCTION

The prairies and oak savannas of the Willamette Valley-Puget Trough-Georgia Basin (WPG) ecoregion are increasingly rare and are recognized as one of the most endangered ecosystem types in North America (Noss et al. 1995, Floberg et al. 2004, Stanley et al. 2008, Dunwiddie and Bakker 2011). Land use changes, habitat fragmentation and invasion by exotics have all contributed to the decline of both the extent and functionality of these habitats (Fimbel 2004, Grosboll 2004, Stanley et al. 2008), and many obligate species have become imperiled as a result (Dennehy et al. 2011, Hamman et al. 2011, Schultz et al. 2011, Wold et al. 2011). Among these are the Taylor's checkerspot butterfly (*Euphydryas editha taylori*), and golden paintbrush (*Castilleja levisecta*).

Euphydryas editha taylori is a non-migratory butterfly that has been federally listed as a potentially endangered species (2012). It once flourished on glacial outwash prairies, low elevation grassy balds and coastal grassland sites from southern British Columbia to central Oregon (Grosboll 2004, Schultz et al. 2011, Severns and Grosboll 2011). However, in recent decades habitat loss and degradation have reduced it to only eight isolated populations (Stinson 2005, Schultz et al. 2011). Exacerbating the threat to *E. e. taylori* populations is the declining presence of native forbs (historically the most important food and nectar plants for the species) on remnant prairies (Stanley et al. 2008, Dunwiddie and Bakker 2011), which inhibits the ability of *E. e. taylori* to recolonize the parts of its range from which it has been extirpated. Also, many native prairie plants are now restricted to more xeric sites due to competition with invasive exotics (Fimbel 2004), which may be problematic because early host plant senescence has been shown as a primary source of mortality for pre-diapause *Euphydryas editha* larva (Mackay 1985).

At present, *E. e. taylori* primarily utilizes the introduced exotic, lance-leaf plantain (*Plantago lanceolata* L.) for oviposition. One reason for this is that *E. e. taylori* utilizes an unpalatability defense, by ovipositing selectively on plants which contain iridoid glycosides (Grosboll 2004, Schultz et al. 2011). Upon hatching, the larvae consume these monoterpenes, sequestering them in their tissues and ultimately discouraging predation throughout their life cycle (Bowers 1981). *Plantago lanceolata* contains iridoid glycosides, as do the three native plants that *E. e. taylori* is known to oviposit on harsh paintbrush (*Castilleja hispida* Benth.), shortspur seablush (*Plectritis congesta* (Lindl.) D.C.), and maiden blue-eyed Mary (*Collinsia parviflora* Lindl.), yet due to the decreasing abundance of the native species and the spatial density of *P. lanceolata* patches, *E. e. taylori* has come to be almost completely dependent on this exotic plant (Severns and Warren 2008).

The fact that *E. e. taylori* has switched hosts to a potentially invasive exotic plant presents a problem for restoration management. The introduction of potentially invasive *P. lanceolata* to otherwise high quality native prairie is problematic for land managers, but few other options exist at present. The native plants known to be occasional larval hosts to *E. e. taylori* typically senesce on WPG prairies before *E. e. taylori* larvae are able to successfully enter diapause (Mary Linders, personal communication). In contrast to the natives, *P. lanceolata* often persists throughout the summer.

An ideal host plant for *E. e. taylori* would, 1) contain an suitable array of iridoid glycosides to be chosen for oviposition, 2) provide enough biomass to support prediapause larva into the third instar when they begin to disperse, and 3) persist long enough to allow larvae to successfully enter diapause. The only plant currently available to *E. e. taylori* on WPG prairies, which possesses all three of these qualities, is *P. lanceolata*.

One native plant which shows promise as a larval host is another federally-threatened species, golden paintbrush (*Castilleja levisecta*). It is an iridoid glycoside-producing perennial which shares with *E. e. taylori* approximate historic range (Wentworth 2001, Lawrence and Kaye 2008, 2011), preferred habitat types, and reasons for population decline. Currently there are no co-occurring populations of *C. levisecta* and *E. e. taylori*. Because of this, it is unknown if *E. e. taylori* will oviposit on *C. levisecta*, but it is recognized that in several ways it might be highly suitable. For example, *C. levisecta* occupies slightly more mesic microsites than the known native hosts and it often persists well into the summer months (Wentworth 2001). Additionally, the growth form of *C. levisecta* may provide more available biomass for larval consumption than *C. hispida,* so it might be able to host larger populations per plant. These characteristics of *C. levisecta*, in addition to the relatively coincident decline of both species, has led to speculation that *C. levisecta* could be an ancestral host for *E. e. taylori* (Stinson 2005).

Despite its potential suitability, *C. levisecta* has not been experimentally reintroduced to *E. e. taylori* habitat sites because congeneric *C. hispida* is actively planted at these locations and the two species could hybridize if grown together (Lawrence and Kaye 2008). Research is currently ongoing to address the question of hybridization rates, but until these are known, the reintroduction of *C. levisecta* at *E. e. taylori* restoration sites would require replacing *C. hispida* entirely, and that may present too much of a risk prior to verification of its suitability as a host plant. In the interim, *C. levisecta* is reintroduced at separate restoration sites; however, if it could be shown that *E. e. taylori* will select *C. levisecta* for oviposition, the two recovery efforts might be joined, potentially increasing the effectiveness of both efforts.

To assess the viability of *C. levisecta* as a host plant, we undertook a manipulative oviposition preference study to compare the likelihood of it being selected by *E. e. taylori* from among *C. hispida* and *P. lanceolata*. Our hypotheses were that 1) the two native *Castilleja* spp. would be preferred over *P. lanceolata* due to their historical coexistence with *E. e. taylori*, and 2) *C. levisecta* would be the most preferred overall due to its potential suitability as a host plant and the possibility of an unknown historical interaction.

METHODS

Site description

Research was conducted in a purpose-built butterfly breeding facility at Mission Creek Corrections Center for Women (MCCCW) in Belfair, Washington, USA, under the guidance of the Sustainability in Prisons Project (SPP). The SPP is a collaboration between The Evergreen State College (TESC) and the Washington Department of Corrections (WDOC) which seeks to engage incarcerated men and women in science, conservation, and sustainability, in order to reduce the environmental, social, and human costs of prisons (LeRoy et al. 2012).

The butterfly facility is a 3 x 7.3 m partitioned greenhouse with UV-transmitting glass panels. Research was conducted in the smaller of two rooms (3 x 2.4 m) while normal rearing and breeding activities were confined to the larger. Trained inmate butterfly technicians performed all research activities, with daily oversight by a graduate and two undergraduate students. In keeping with the SPP's mission, inmate technicians were engaged as collaborators and were involved in many phases of the work, including: planning, methods refining, data collection, and manuscript review.

Data Collection

Methods for testing oviposition preference were developed with California populations of *E. editha* (Singer 1982, Singer et al. 1991, 1992), and with *Melitaea cinxia* (Singer and Lee 2000). These methods were designed to compare preference between just two potential hosts. We made pairwise comparisons among *C. levisecta*, *C. hispida*, and *P. lanceolata* for a total of three complete comparison sets. Each comparison involved 10 individual trials, each with a different butterfly selected randomly from five different captively-reared lineages.

Butterflies were F_1 descendants of individual wild-caught females, collected from Range 76 on Joint Base Lewis-McChord in 2011. This site hosts the species' largest extant population, and currently supports the collection of all captive colony founders.

In general, oviposition preference testing is possible because the butterflies display behaviors that indicate selection prior to oviposition (Singer

1982). Upon alighting on a potential host, the butterflies taste for the presence of iridoid glycosides with specially adapted fortarsi. If conditions are not adequate they will not oviposit and move to another location. Butterflies often decline or accept different individuals of the same species, apparently selecting for an unknown but specific chemical signature. If the butterfly approves of the potential host's alkaloid signature, she may tap her antennae or wave her wings in further investigation before finally curling her abdomen and touching her ovipositor to the plant, indicating final oviposition selection.

Following Singer (1982, Singer et al. 1991, 1992, Singer and Lee 2000), oviposition preference was determined by sequentially offering individual gravid females (n=30), test plant individuals (n=3) of two species per comparison (Figure 1). Each plant was contained within a small screen enclosure. The butterflies, which were not initially motivated to oviposit, were placed into an enclosure with a randomly chosen plant and observed for five minutes for oviposition behavior, before being offered the next plant. After a positive attempted oviposition, which was denoted by the female touching her ovipositor to a leaf surface for two seconds, she was placed in an empty enclosure for five minutes before being offered the next plant. Testing sessions continued until females chose all six plants. They were then allowed to oviposit completely in a separate enclosure, on the plant of highest preference.

Three plants of each species were used in each trial to account for within-species variation in alkaloid signatures. Plants were randomly selected for each trial from pools of 80 individuals. The plants were all in reasonably good health,

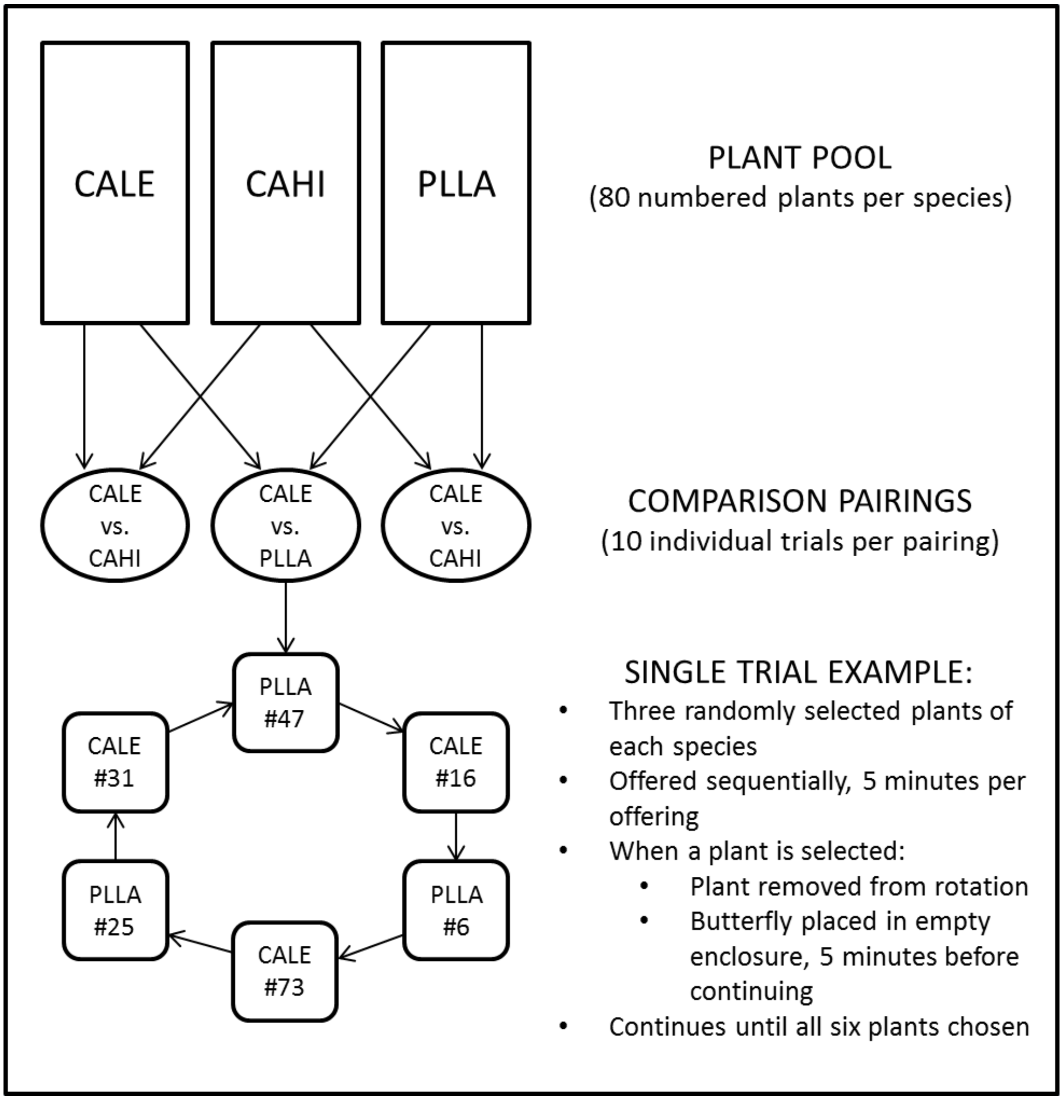

Figure 1 – Details of oviposition preference testing methods carried out at the endangered butterfly rearing facility at Mission Creek Corrections Center for Women, Belfair, Washington, USA

and each selected individual was used only in a single trial. Plants were all from south Puget lowland genetic stock, and were grown under similar conditions. These plants were propagated from the same populations used for Taylor's checkerspot restoration efforts. The butterflies themselves are also from the same lineages that are reared for release on south Puget lowland prairie restoration sites.

Throughout the trials, temperature was maintained within a range of 24-32 °C. Other environmental variables were assumed to be relatively standardized due to the randomized pairings. Over 1200 individual five-minute trials were performed during the course of the study.

Statistical Analysis

Preference between potential hosts for each butterfly was assessed by averaging the rank of acceptance. For example if, during a trial between *C. levisecta* and *C. hispida*, *C. levisecta* was selected first, second, and fourth, it would be given a score of 2.33. We call this statistic the mean selection rank, and lower selection ranks indicate higher preference. Additionally, accepted plants were only considered preferred if the next plant offered was declined, so plants accepted sequentially were given the same averaged rank, creating the possibility of a given trial resulting in no preference shown for either species. Overall preference between plant species was determined by comparing the overall means of all three comparisons using a one-way ANOVA and Tukey's HSD test.

RESULTS

Comparison of mean selection rank (Figure 2) showed that *E. e. taylori* did not equally prefer the three plants ($F_{(2,27)} = 18.02$, $p<0.0001$). Post-hoc tests revealed that the two *Castilleja* spp. were preferred equally, but each was preferred over *P. lanceolata*.

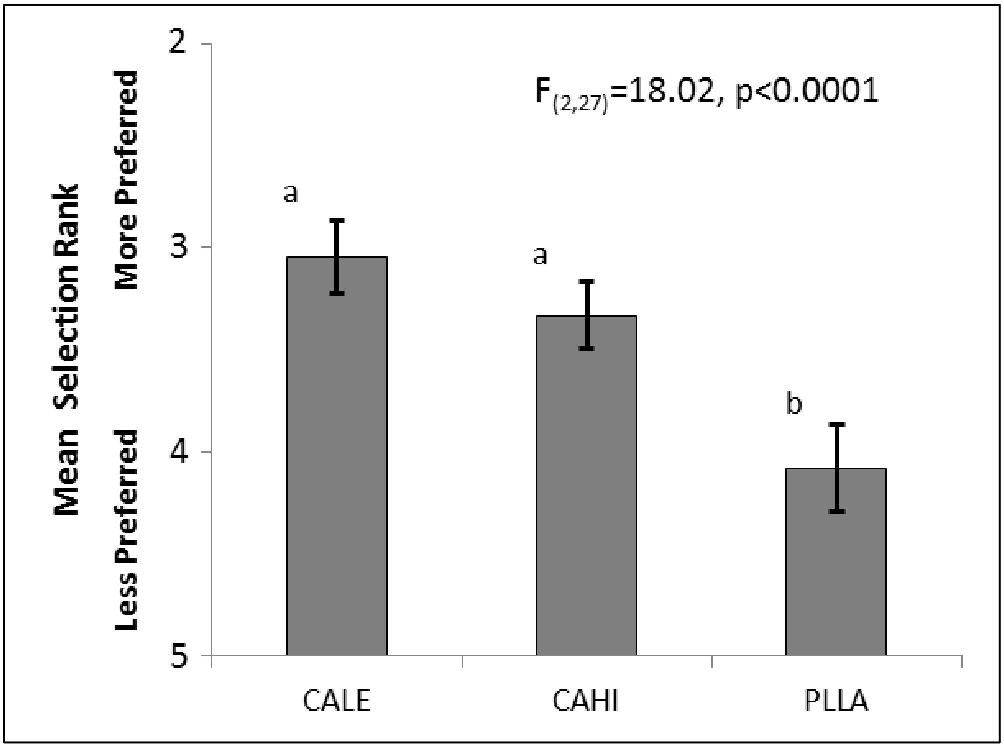

Figure 2 – Mean oviposition preference among potential host plants. Each trial resulted in a mean selection rank based on selection order of the six plants offered, resulting in a score between two and five with low scores indicating higher preference.

The record of individual trial results (Figure 3) shows that for the 10 butterflies offered the *C. levisecta* and *P. lanceolata* pairing, nine preferred *C. levisecta* and one showed equal preference for both. Between *C. hispida* and *P. lanceolata*, seven preferred *C. hispida*, one preferred *P. lanceolata,* and two showed equal preference for both. Between the two *Castilleja* spp., four preferred *C. levisecta*, three preferred *C. hispida*, and three showed equal preference for both.

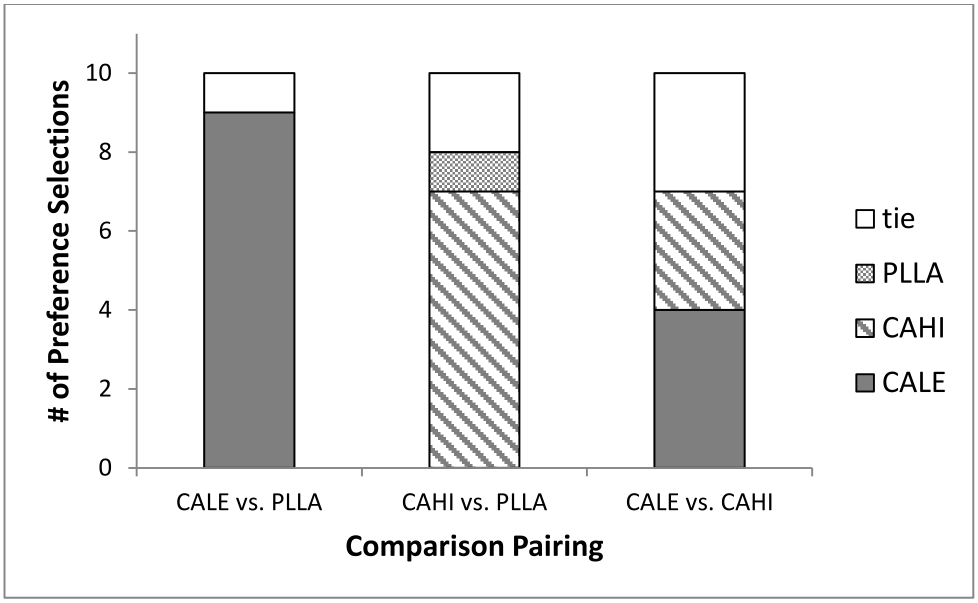

Figure 3 – Results of the 10 trials in each oviposition preference comparison pairing.

DISCUSSION

Our results not only show that *E. e. taylori* will select *C. levisecta* for oviposition, but that its preference for *C. levisecta* is equal to its preference for *C. hispida*, the most suitable of the currently known native host plants. Adding another suitable native host to the *E. e. taylori* reintroduction site planting mix may increase the effectiveness of recovery efforts.

Both *Castilleja* spp. were preferred over *P. lanceolata* despite the fact that the butterflies had consumed *P. lanceolata* exclusively as larvae. This can be explained by research with the conspecific bay checkerspot (*Euphydryas editha bayensis*), which found that oviposition preference was heritable (Singer 1988). Singer's research with *E. e. bayensis* (1988) also showed that oviposition preference was correlated with offspring growth rate, indicating that a mother's use of her preferred oviposition host conferred an advantage to her offspring.

Since the two *Castilleja* spp. in our study were preferred over *P. lanceolata*, it is possible that *E. e. taylori* is at a disadvantage when utilizing *P. lanceolata*, its most common larval host.

The observed trend in oviposition preference of *C. levisecta* over *C. hispida*, as indicated by mean selection rank, was non-significant. However, the mean score for *C. levisecta* was higher than for *C. hispida*, a trend corroborated by the record of individual trial results. Because of this, we suspect that a larger sample size might have shown *C. levisecta* to be the most preferred host overall; further inquiry will be required to investigate this.

More work also needs to be done in the field to determine the efficacy of *C. levisecta* as a larval host, but if it could be utilized in *E. e. taylori* reintroduction site plantings, either alongside or in place of *C. hispida*, the effectiveness of two threatened species recovery efforts might be synergistically increased. The potential exists to provide a valuable native host to *E. e. taylori* while also creating more planting sites and a more robust metapopulation for *C. levisecta*. In an age of ambitious conservation goals and limited resources, efficiency is paramount to overall success.

In a novel collaboration, we have found that the effective employment of non-traditional partners, in this case incarcerated women, can also help increase the available resources for conservation and improve overall efficiency. We hope that our project opens doors to more collaborative conservation science in correctional facilities and other non-traditional environments in the future.

Acknowledgments

The butterfly facility at Mission Creek Corrections Center for Women is managed by the Sustainability in Prisons Project and Washington Department of Corrections staff, overseen by the Washington Department of Fish and Wildlife, assisted by the endangered butterfly lab at Oregon Zoo (Portland, Oregon), and funded by a US Fish and Wildlife Grant through the US Army Compatible Use Buffer program. We thank these partners, The Evergreen State College, and WDOC administration for their support of both this research and the overarching vision of science in prisons. We also thank the individuals that helped make this research a reality: Kelli Bush, Joslyn Trivett and Carl Elliott from SPP, undergraduate interns Caitlin Fate and Chelsea Oldenburg from TESC, Superintendent Wanda McRae, Anne Shoemaker, Leo Gleason, Sherri Albrecht, and Dan Davis from MCCCW, Ted Thomas of the U.S. Fish and Wildlife Service, Mary Jo Andersen and Karen Lewis of the Oregon Zoo, and and five inmates, who will remain unnamed, that supported and participated in gathering these data..

REFERENCES

Bowers, M. D. 1981. Unpalatability as a defense strategy of western checkerspot butterflies (*Euphydryas scudder*, Nymphalidae). Evolution 35:367–375.

Dennehy, C., E. R. Alverson, H. E. Anderson, D. R. Clements, R. Gilbert, and T. N. Kaye. 2011. Management strategies for invasive plants in pacific northwest prairies, savannas, and oak woodlands. Northwest Science 85:329–351.

Dunwiddie, P. W., and J. D. Bakker. 2011. The future of restoration and management of prairie-oak ecosystems in the Pacific Northwest. Northwest Science 85:83–92.

Fimbel, C. 2004. Habitat enhancement for rare butterflies on Fort Lewis prairies. Report to The Nature Conservancy, South Sound Office, Olympia Washington.

Floberg, J., M. Goering, G. Wilhere, C. MacDonald, C. Chappell, C. Rumsey, Z. Ferdana, A. Holt, P. Skidmore, T. Horsman, E. Alverson, C. Tanner, M. Bryer, P. Lachetti, A. Harcombe, B. McDonald, T. Cook, M. Summers, and D. Rolph. 2004. Willamette Valley-PugetTrough-Georgia Basin ecoregional assessment. The Nature Conservancy with support from the Nature Conservancy of Canada, Washington Department of Fish and Wildlife, Washington Department of Natural Resources (Natural Heritage and Nearshore Habitat programs), Oregon State Natural Heritage Information Center and the British Columbia Conservation Data Centre.

Grosboll, D. N. 2004. Captive rearing the endangered mardon skipper (*Polites mardon*) and Taylor’s checkerspot (*Euphydryas editha taylori*) butterflies: Initial results (Lepidoptera, Nymphalidae). Proceedings of the Species at Risk Pathways to Recovery Conference, Victoria, B. C.

Hamman, S. T., P. W. Dunwiddie, J. L. Nuckols, and M. McKinley. 2011. Fire as a restoration tool in Pacific Northwest prairies and oak woodlands:

Challenges, successes, and future directions. Northwest Science 85:317–328.

Lawrence, B. A., and T. N. Kaye. 2008. Direct and indirect effects of host plants: Implications for reintroduction of an endangered hemiparasitic plant (*Castilleja levisecta*). Madroño 55:151–158.

Lawrence, B. A., and T. N. Kaye. 2011. Reintroduction of *Castilleja levisecta*: Effects of ecological similarity, source population genetics, and habitat quality. Restoration Ecology 19:166–176.

LeRoy, C. J., K. Bush, J. Trivett, and B. Gallagher. 2012. The Sustainability in Prisons Project: An overview (2004-12). Gorham Printing, Olympia, Wa.

Mackay, D. A. 1985. Conspecific host discrimination by ovipositing *Euphydryas editha* butterflies: Its nature and its consequences for offspring survivorship. Researches on Population Ecology 27:87–98.

Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. Report to the US Department of the Interior, National Biological Service, Washington D. C.

Schultz, C. B., E. Henry, A. Carleton, T. Hicks, R. Thomas, A. Potter, M. Collins, M. Linders, C. Fimbel, S. Black, H. E. Anderson, G. Diehl, S. Hamman, R. Gilbert, J. Foster, D. Hays, D. Wilderman, R. Davenport, E. Steel, N. Page, P. L. Lilley, J. Heron, N. Kroeker, C. Webb, and B. Reader. 2011. Conservation of prairie-oak butterflies in Oregon, Washington, and British Columbia. Northwest Science 85:361–388.

Severns, P. M., and D. Grosboll. 2011. Patterns of reproduction in four Washington State populations of Taylor's checkerspot (*Euphydryas editha taylori*) during the spring of 2010. Report to The Nature Conservancy, Olympia, Washington.

Severns, P. M., and A. D. Warren. 2008. Selectively eliminating and conserving exotic plants to save an endangered butterfly from local extinction. Animal Conservation 11:476–483.

Singer, M. C. 1982. Quantification of host preference by manipulation of oviposition behavior in the butterfly *Euphydryas editha*. Oecologia 52:224–229.

Singer, M. C., and J. R. Lee. 2000. Discrimination within and between host species by a butterfly: Implications for design of preference experiments. Ecology Letters 3:101–105.

Singer, M. C., D. Ng, and R. A. Moore. 1991. Genetic variation in oviposition preference between butterfly populations. Journal of Insect Behavior 4:531–535.

Singer, M. C., D. Ng, and C. D. Thomas. 1988. Heritability of oviposition preference and its relationship to offspring performance within a single insect population. Evolution 42:977-985.

Singer, M. C., D. Vasco, C. Parmesan, C. D. Thomas, and D. Ng. 1992. Distinguishing between "preference" and "motivation" in food choice: An example from insect oviposition. Animal Behaviour 44, Part 3:463–471.

Stanley, A. G., T. N. Kaye, and P. W. Dunwiddie. 2008. Regional strategies for restoring invaded prairies. Native Plants Journal 9:247 –254.

Stinson, D. W. 2005. Draft status report for the Mazama pocket gopher, streaked horned lark, and Taylor's checkerspot. Report to the Washington Department of Fish and Wildlife, Olympia, Washington.

Wentworth, J. B. 2001. The demography and population dynamics of *Castilleja levisecta*, a federally threatened perennial of Puget Sound grasslands. *In* R. S. Reichard, P. Dunwiddie, J. Gamon, A. Kruckeberg, and D. Salstrom, editors. Conservation of Washington's Native Plants and Ecosystems. Washington Native Plant Society, Seattle, Washington.

Wold, E. N., J. E. Jancaitis, T. H. Taylor, and D. M. Steeck. 2011. Restoration of agricultural fields to diverse wet prairie plant communities in the Willamette Valley, Oregon. Northwest Science 85:269–287.

DISCUSSION & BROADER IMPACTS

ECOLOGICAL IMPLICATIONS

Taylor's checkerspot

One of the problems facing *E. e. taylori* conservation is a lack of firm understanding surrounding which plants are the species' most important native oviposition hosts. Currently the butterfly almost exclusively utilizes *P. lanceolata*, which is a potentially invasive exotic species, for oviposition. Several native plants are known to be occasional larval food sources, but oviposition hosts are more strategically valuable than other food plants. By laying their eggs in clutches, *E. e. taylori* females are essentially choosing individual plants which will support her young through their first few instars. The literature is unclear about which plant species were historically the most important for *E. e. taylori*, in part because *P. lanceolata* has been abundant on WPG prairies for so long. It was reportedly common around Fort Vancouver by 1825 (Nisbet 2009). The historical and current abundance of *P. lanceolata,* and the degree to which it is utilized, make it difficult to describe *E. e. taylori*'s most important native plant interactions.

Another reason it is difficult to understand the historical web of native species interactions is the lack of some plant species, like *Castilleja levisecta*, that once occupied similar historic ranges with *E. e. taylori*, but now do not. Many species have been impacted by the loss, fragmentation, and degradation of WPG prairie habitat.

It is likely we will never know for sure what the most important native plants were for *E. e. taylori* prior to the arrival of *P. lanceolata*, but the results of this research may provide clues to the mystery. Both *Castilleja* spp. were preferred for oviposition over *P. lanceolata*. It may be that these were important ancestral host plants for *E. e. taylori*.

Because the prairies with the richest soils were typically the first to be converted to agriculture, many native plants have been pushed to the edges of their preferred range. It may be that the *Castilleja* spp. are less suitable as larval hosts for *E. e. taylori* when growing on more xeric soils. Early host plant senescence has been shown to be a primary cause of mortality for pre-diapause *E. e. bayensis* larvae (Ehrlich 1961, Mackay 1985, Grosboll 2011), and in some cases small variations in soil moisture have been shown to have large impacts on larval survival (Singer 1972, Weiss et al. 1988). Native host plants are more likely to senesce before the caterpillars are able to safely enter diapause if they are growing in marginal habitat. Because of this, it could be argued that *P. lanceolata* may have been both bane and boon to *E. e. taylori's* persistence. It is a bane in that exotic species are influential in pushing natives to the fringe in the first place, but a boon in being an acceptable surrogate for *E. e. taylori* larvae in the absence of suitable native host populations.

The suitability of *P. lanceolata* as a larval host stems from three factors. First, it is much less prone to desiccation than any of the known native hosts. It often persists well into autumn, so it is almost guaranteed not to senesce before *E. e. taylori* larvae enter diapause in early July. Second, it contains iridoid glycosides, similar to those found in the known native hosts, which *E. e. taylori* sequester in their tissues to maintain their unpalatability defense. Third, *P. lanceolata* individuals are well distributed and tend to exist in dense enough populations that they both: 1) are relatively likely to be found by gravid *E. e. taylori* females, and 2) can support lots of hungry dispersing caterpillars.

Despite the fact that *P. lanceolata* provides key resources for *E. e. taylori*, there are problems associated with planting it at prairie restoration sites. Plots designated for reintroduction of the butterfly are typically stocked with known larval hosts and nectar plants, but the idea of planting a potentially invasive exotic species on high quality native prairie is problematic. Since invasive behavior is often triggered by the crossing of an unknown population threshold (Crooks and Soule 2001, Sakai et al. 2001), land managers must be cautious in deciding how many *P. lanceolata* plants represent the ideal balance between function and risk.

Our results show that *C. levisecta* is preferred by *E. e. taylori* for oviposition over *P. lanceolata*. If future research continues to suggest that *C. levisecta* would be a valuable addition to the suite of native plants used in *E. e. taylori* recovery efforts, it might be possible to reduce the number of *P. lanceolata* individuals needed at reintroduction sites. This, in turn, could reduce the likelihood of *P. lanceolata* crossing a hidden population threshold at any given site and initiating outbreak conditions. Although *P. lanceolata* is known to be invasive in a wide variety of habitat types, including south Puget lowland prairies, it might be possible to slow its spread if planting densities are kept low.

Golden paintbrush

Like *E. e. taylori*, *C. levisecta* is a federally threatened species. Also like *E. e. taylori*, it has a recovery plan, restoration sites, and facility-based cultivation projects for generating reintroduction stock.

Being a known and potentially valuable larval host for *E. e. taylori* may benefit *C. levisecta*. If *C. levisecta* is utilized in restoration plantings for the butterfly, it could increase the total number of *C. levisecta* plugs planted every year, and increase the total number of its recovery sites. Furthermore, the species interaction between *E. e. taylori* and *C. levisecta* may increase public awareness of both species, as people interested in one will be more likely to learn about the other and the synergy the two share. Public awareness, in turn, is critical in determining funding priorities and community support.

Synergy in conservation may also have value of its own accord. As with most activities that do not generate profit, ecological restoration and threatened species conservation are limited by funding and volunteer support. If two threatened species can be conserved synergistically, such limiting resources can be used more efficiently, and the net effort can be made more effective. These outcomes could lead to more total effort for the two species in question, or it could preserve resources for use by other projects.

COLLABORATION

Sustainability in Prisons Project

The Sustainability in Prisons Project (SPP) is a partnership between The Evergreen State College (TESC) and the Washington Department of Corrections (WDOC). It strives to involve incarcerated persons in science, sustainability, and conservation, while engaging them as colleagues and stakeholders, for the sake of ecological and social restoration.

The SPP began in 2004 with a science and sustainability lecture series that spawned several sustainability projects at Cedar Creek Corrections Center (CCCC), a minimum-security men's prison near Littlerock, Washington. Waste sorting, composting, recycling, gardening, rainwater recapture, and even a green roof project, all began from the inspiration of the SPP lecture series. Many of these ideas then quickly caught on at other Washington prisons, first when local media started covering the efforts, and then even more so when it became known how much money CCCC was saving.

The sustainability initiatives inspired by the SPP lecture series are now for the most part carried forward under the broader umbrella of WDOC Sustainable Operations (in partnership with SPP). Direction for these measures happens at both the statewide and the individual facility level. Sustainability in Washington prisons has taken a life of its own, and is one reason why the state is now recognized as a world leader in the greening of corrections (LeRoy et al. 2012). Between 2005 and 2010, WDOC reduced solid waste to landfills by 35%, increased diversion to recycling by 89%, increased composting operations by

90%, decreased potable water use by over 100 million gallons annually, reduced transportation fuel consumption by 25%, and reduced total carbon emissions by approximately 40%. In addition, in 2010 prison gardens and farms yielded over 123,000 kg of produce for consumption by inmates and donations to food banks (LeRoy et al. 2012).

Meanwhile, the science and sustainability lecture series continues and has expanded to five prisons. Bringing informal science and environmental education into prisons remains a priority for the SPP. More than 100 lectures and 26 workshops have been held at five prisons, involving 2400 inmates and 280 WDOC staff attendees (LeRoy et al. 2012).

In 2008, another SPP program was added. A partnership with the Washington Department of Fish and Wildlife (WDFW) allowed CCCC to become a rearing institution for Washington State endangered Oregon spotted frogs (*Rana pretiosa*). These were reared for release onto wetland sites at Joint Base Lewis-McChord, with professional biologists from other rearing institutions such as the Woodland Park Zoo and the Oregon Zoo working collaboratively with inmates from CCCC. When the project began, there was some debate about whether the inmates would be able to match the success of professional rearing institutions, but those doubts were soon erased. The CCCC frog program had the highest survivorship and most developed frogs of any institution, and was named "best rearing facility" in 2009, 2010, and 2011. Additionally, inmates participated in conducting relevant research including a growth comparison between two distinct frog populations with WDFW, and a predator evasion response experiment with the Oregon Zoo.

The following year in 2009, the SPP began a rare and endangered prairie plant propagation program at Stafford Creek Corrections Center (SCCC), a medium-security men's facility near Aberdeen. It employs up to 10 inmates and has produced over 600,000 plants for south Puget Sound restoration sites both on and off JBLM. The SPP recently doubled the capacity of this program by adding a similar program at the Washington Corrections Center for Women (WCCW), a medium-security facility near Gig Harbor.

In an added layer of synergy, many of the plants raised at SCCC and WCCW are planted on *E. e. taylori* restoration sites. These sites now host butterflies raised by inmates at the Mission Creek Corrections Center for Women (MCCCW), a minimum security prison near Belfair

Like the other SPP conservation projects, the butterfly program at MCCCW is made possible by a diverse assemblage of collaborating partners. The facility, a purpose-built 3 x 7.3 m partitioned greenhouse with UV-transmitting glass panels (Plates 1 & 2), was built with a US Fish and Wildlife Service (USFWS) grant, using funds from the Department of Defense's Army Compatible Use Buffer (ACUB) program. Captive rearing activities are supported by WDFW and the Native Butterfly Conservation Lab at the Oregon Zoo. Funds for the overall *E. e. taylori* recovery effort also come from ACUB and USFWS, and are overseen by WDFW.

Plate 1 – Butterfly rearing facility at MCCCW, with flying shade cloth, winter diapause shed, and raised garden beds for larval food plants

Plate 2 – Mary Jo Andersen of the Oregon Zoo working with inmates inside the greenhouse at the beginning of the 2012 rearing season

Inmates at MCCCW helped build the butterfly greenhouse in 2011, and then were trained to care for butterflies using painted ladies (*Vanessa cardui*) as a training surrogate. These butterflies have short life cycles and are very forgiving in terms of the conditions that they require for survival. Therefore, inmates were able to use the *E. e. taylori* rearing and breeding protocols developed by the Oregon Zoo, practicing through five complete life cycles before ever seeing a Taylor's checkerspot. When the *E. e. taylori* rearing season began, the inmates quickly proved that the trust placed in their abilities by all of the funding and conservation partners was well warranted. In 2012, 701 checkerspots were released into the wild, 92 successful breeding introductions were made, resulting in 3,624 pre-diapause larvae (180% of the pre-season target), and an egg-to-diapause survivorship of 96.6%. The end of the rearing season is in early July when the animals go into diapause, whereupon the bulk of them were taken to the established diapause area at the Oregon Zoo. The other 500 were kept at MCCCW over the winter as a trial. Of these, 100% survived. The entire cohort was returned to MCCCW in late February for wake-up, after which 3400 were released, bringing the total number of *E. e. taylori* individuals restored to the prairie so far by MCCCW to over 4,000.

The success of the project can be attributed to at least three things: the inmates, the facility, and the collaboration. The inmate butterfly technicians at MCCCW have been meticulous, careful, thorough, and dedicated. They have taken ownership of the project and its goals, they go out of their way to do things better, and they keep records over and above what they have been asked to keep.

In some cases they have developed new methods to do things that have been incorporated into protocols at the Oregon Zoo. Other times they have learned things such as, if you rub the feet of a butterfly from the outside of its screen enclosure it will bask its wings contentedly. At the end of the flight season in 2012, they took it on themselves to give hospital-like care to the older butterflies, hand-feeding them honey water from tiny spoons. The point is, they have time on their hands to do this work as thoroughly as can be imagined.

The second reason for the success of the project has been the facility. One of the limiting variables at the Oregon Zoo facility is natural light. The *E. e. taylori* rearing facility at the Oregon Zoo is housed in what was formerly a giant air-conditioning unit for polar bears. They have two small windows to let in natural light, which is important for butterfly life-stage cues and development. Most of the time the butterflies have to make due with supplemental lighting on timers. For breeding, staff have to hang them in small enclosures in front of the windows, and then hope that clouds do not block the sun. At MCCCW, there is so much light in the facility that breeding can be accomplished on the most miserably drizzly overcast Washington day. The enclosures are hung near the roof, the heat is cranked up, and the butterflies waste no time copulating as if it were a hot sunny day on the prairie.

The third reason for the success of the MCCCW butterfly rearing facility is the collaboration among numerous partners. The work would not be possible without all the groups working together. The Department of Defense paid for the facility, USFWS oversaw the funds, WDFW provides overarching project leadership, training and rearing support comes from the Oregon Zoo, there is a graduate student coordinator as well as faculty and staff support from SPP/TESC, funding and staff support from WDOC, and the inmates themselves; all of these partners play crucial roles in this truly synergistic conservation effort.

Value of collaborative conservation

Collaborative conservation has been identified as a rising phenomenon (Brick et al. 2001, Lauber et al. 2011) which often provides significant benefits to multiple partners. It can help involve community partners who might not otherwise contribute, bridge the information divide between scientists and citizens, and foster sharing of resources such as funding and labor. Additionally, multiple partners can increase overall effectiveness by allowing partner groups to work within their strengths. Furthermore, partners can reap the benefits of other groups' strengths and the services they provide.

The butterfly program at MCCCW is an excellent example of collaborative conservation. Every partner benefits and the net result is a more effective effort than any group could accomplish alone. It has been described as a 5-way win-win situation: WDFW gets a second rearing facility where inmates do professional work at a fraction of the cost, the Oregon Zoo enjoys greater resilience in its captive colony and increased breeding capacity, WDOC receives valuable programming for its inmates and receives positive media attention, TESC is able to provide project management experience to a graduate student and gains a new opportunity for research, and the DOD and JBLM get help restoring a species that threatens to curtail training activities on an important practice range. Other winners are the inmates themselves, who get the opportunity to contribute a valuable service to society, are provided an environment where they can do rehabilitative self-work while nurturing living beings, enjoy a collegial relationship with academics and conservation professionals, and are exposed to science and laboratory techniques for possible future study or employment.

Every partner wins. Every group is enjoying a success they could never achieve alone. No matter how success is measured, the collaboration takes the efforts of each partner and returns an emergent triumph. A prison raises endangered butterflies, an army base gets to keep training with live artillery, a state conservation agency doubles its output with negligible increase in cost, and a college known for interdisciplinary learning puts a student right in the middle of all of it; none of these benefits would be possible without the collaboration.

SOCIAL IMPLICATIONS

Transforming prisons

A retributive criminal justice paradigm has been historically prevalent in the United States and around the world, and has largely continued to be so into the present. Beginning in the 1990's, however, increasing investments were made in skill-building and re-entry programs, reflecting a shift toward a more restorative criminal justice system (Phelps 2011).

The retributive and restorative justice paradigms are philosophically very different in several important ways, as described in the criminal justice literature

(Wenzel et al. 2008, Dancig-Rosenberg and Gal 2013). Retributive justice attempts to solve rule-breaking through punishment and the threat of punishment. Interaction is one-directional, a power and status disparity is implied, and an individualistic mentality is encouraged. Conversely, restorative justice attempts to solve rule-breaking through rehabilitative programming and reinforcing the offender's role in society. Interaction is bi-directional, the value of every member of society is implied, and a focus on community contribution is encouraged.

Retributive and restorative criminal justice paradigms both attempt to solve the same societal problem, but they do so in nearly opposite ways, leading some to claim that they may work against each other (Bazemore 1998). This idea holds that rehabilitative programming may soften the effects of punishment, and punishment may lessen the effects of rehabilitation. This concept of polarity is one of the standard arguments for those who consider punishment-only incarceration the best model. Since the retributive justice paradigm continues to be the undeniable foundation of incarceration, this sentiment is not uncommon within the prison system itself.

Organizations like SPP, however, are proud to champion the growth of restorative justice, and believe that rehabilitative programming does the opposite of limiting the effectiveness of punishment. It works with rather than against incarceration and adds to the functionality of the justice system as a whole, while also tending to increase prison safety at the same time (LeRoy et al. 2012). This way of thinking is borne out by more recent criminal justice literature. An upcoming article in the Carrozo Law Review (Dancig-Rosenberg and Gal 2013) redefines the role of retributive justice by placing punishment as a useable tool in a larger restorative framework.

Under the restorative justice paradigm, the long-term goal of corrections is founded in the assumption that inmates serve their time and then return to our communities to become our neighbors again. Reports have shown that purely punitive penal systems do not do an efficient job rehabilitating people, and are in fact often more likely to “lead to more crime following release” (Chen and Shapiro 2007). Harsher sentences have been correlated with poorer post-release employment rates (Western et al. 2001), while prison stays have been shown to increase introversion and violent tendencies (Bolton et al. 1976), and peer-to-peer social interaction in prison has been linked to an evolution of criminal tendencies, or a crime learning effect (Glaeser et al. 1996, Bayer et al. 2004). If the goal of corrections is to get people back on track so that they can become functional members of our society, then a different approach is needed.

Rehabilitative programming can take many forms. If the measurement of rehabilitative success is getting people back on their feet and functioning in society, then the most direct methods are programming elements that have been shown empirically to reduce recidivism such as formal education and re-entry job skills training. Other types of programming which also can be considered rehabilitative include informal education, opportunities for offenders to contribute to the outside community, and activities that decrease negative emotions during incarceration (such as gardening or access to a library).

If there is a weakness in the effectiveness of the SPP's conservation programs in terms of rehabilitation, it is that emphasis on developing marketable skills for the post-release job market is not the primary focus. That said, every other category of rehabilitative programming is covered. At MCCCW, a wide range of environmental and scientific topics are discussed by inmate butterfly technicians and the TESC graduate student overseeing the project, during extra time budgeted every week for that purpose. In addition, several lectures have been brought to MCCCW for the general population to increase education about butterflies.

Opportunities to contribute meaningfully to the larger community are also considered important for rehabilitation. The butterfly technicians at MCCCW are able to play an integral part in efforts to restore a federally threatened pollinator to south Puget lowland prairies. Furthermore, they are helping conduct relevant research and contributing to the body of scientific literature about the species they work with. In fact, in the case of the oviposition preference study, two of the technicians were so involved and took such ownership that they earned spots as co-authors on the scientific manuscript being prepared for peer-reviewed publication. Also, before the study there had been no documentation of *E. e. taylori* using *C. levisecta* as an oviposition host at all, so after it was clear that this was indeed happening a camera and macro-lens were brought to the greenhouse. One of the inmates was an avid amateur photographer before her incarceration, and she got to be the first person to document the relationship (Plate 3).

Plate 3 – A Taylor’s checkerspot female ovipositing on golden paintbrush; this photo was taken by an inmate butterfly technician at MCCCW and is the first documentation of this interaction between the two threatened species.

Another opportunity to contribute is that, in a larger sense, the inmates’ success at MCCCW is paving the way for this model to spread. By showing that butterflies and prisons are a good match, and doing so with high success rates, the inmate butterfly technicians are making their program an example to the world. When other states or nations go to sell the idea of endangered butterflies in prison to policy makers and land managers, the MCCCW butterfly program provides evidence that the model works. By working hard, taking ownership, and caring for their charges with delicate patience, they are potentially paving the way for other women to have similar opportunities, in other states, or possibly even around the world. Since 2012, another butterfly program has been started at the

Washington State Penitentiary, and plans are being made for a butterfly rearing program in Oregon.

There are several types of prison programming that are considered rehabilitative, but one of the common themes is the reduction of negative emotions. Typical examples of programming thought to be effective at this are jobs, recreation, gardening, access to books or art supplies, and religious services. I argue that the butterfly program at MCCCW has the potential to reduce negative emotions in several ways. First, working with and nurturing living organisms, then watching them develop and metamorphose into butterflies may be therapeutic, and provides an example of transformation and change for people undergoing changes within themselves. Second, the greenhouse itself is a peaceful environment, outside the fenced yard and all its rush and intensity. The butterfly technicians at MCCCW have reported listening to the caterpillars chew leaves on a quiet sunny afternoon, and have often commented on the meditative quality of the working environment. Next, the SPP is committed to interacting with inmate technicians as colleagues rather than employees. Their ideas are welcomed and often implemented by the facility at the Oregon Zoo. They have the opportunity to sit with a graduate student every week, and discussion is welcomed on any scientific topic they are interested in. Furthermore, the inmates are able to interact with college professors and agency biologists within the framework of a professional relationship. They are even allowed to attend (with custody staff escort) annual working group meetings for the range-wide *E. e. taylori* recovery effort, where they are able to hear presentations and discussions on all the latest ideas, from genetics research to site suitability reports and wild population updates. I argue that the validation and respect inherent in being treated like a partner can also serve to reduce negative emotions and perhaps be rehabilitative.

Community benefits

The reality of reentry is that inmates return home. As discussed above, they finish their sentences and return to our communities, rejoining family and becoming our neighbors. The aspects of prison aimed at rehabilitation are the ones that serve a functional purpose for the future good of society.

The SPP is helping prisons by providing a new avenue for functionality in an increasingly connected and aware society. The benefits of rehabilitative programming were not newly invented by SPP, however. The elegance of the SPP idea is that it brings another social goal, ecological restoration, into the picture. In fact, SPP brings several societal needs to the table at the same time and uses collaboration to address them all. If all aspects of this multi-dimensional community benefit were realized, prisons would be more functional in the community, the military would be able to keep us all safer, conservation efforts would be more effective, students would become better graduates for the working world, and scientific knowledge would increase.

Involving underserved audiences

There is growing emphasis in the scientific community on reaching out from the ivory tower to involve a wider audience in science education (Nadkarni 2004, 2006, 2007, McCallie et al. 2009, Bonney et al. 2009). Benefits of outreach and informal science education may include broader discussions, new ideas, greater community participation, more new student enrollments, and increased interest through media exposure.

Involving inmates in relevant scientific research brings a novel audience into the discussion. Educational programming in prisons has traditionally been almost entirely through high school equivalency, associate's degree programs, and religious learning, but involving inmates in research brings science into the prison community in a new way (Weber 2012). Inmates who participate learn through experience, and may extend the effects of science education by talking to fellow inmates about their jobs.

Other underserved audiences may also benefit from involvement in relevant scientific research, such as people in restrictive institutions like jails, mental institutions, retirement homes, and public schools. The work of forming these partnerships is beyond the scope of SPP, but the model that SPP has created may inspire other groups to seek out such novel collaborations in the future.

AN INTERDISCIPLINARY THESIS

In working for the SPP, coordinating the butterfly program at MCCCW and carrying out this oviposition preference research, many lines of interdisciplinarity were explored, joining conservation biology with environmental education and social justice. I worked within the criminal justice system and helped provide corrections programming while bringing collaborative conservation to an underserved scientific audience. I learned about restoration ecology on butterfly release sites, and endangered species protection working with state agencies. I learned how to staff and manage a captive breeding facility, and played a role in a multi-partner collaboration. I participated in informal science education and public outreach, speaking at conferences, community events, and a public elementary school. I would argue that my work with incarcerated women and endangered butterflies, and the oviposition preference research that we did together, reflects a truly interdisciplinary MES thesis.

CONCLUSIONS

In my opinion, the most important implication of the oviposition preference study and its results was that there may now be the opportunity to bring two threatened species together for the mutual benefit of both. If further research continues to indicate that *C. levisecta* would be a suitable oviposition host for *E. e. taylori*, it could be planted at the butterfly reintroduction sites. This unified restoration approach could provide a more diverse assemblage of resources for the animals while reducing the need to plant exotic *P. lanceolata* on high quality native prairie, while at the same time adding planting sites to the *C. levisecta* recovery effort.

The most important aspect of doing this research at MCCCW has been in establishing a successful model for conservation work in prisons, which is being expanded to other situations. By showing that a program like the one at MCCCW can come on-line quickly, and function both effectively and inexpensively, we are paving the way for other similar programs to follow. Our success makes the idea of prisons as conservation partners attractive and easier to sell to policy makers in other states. In the future, I would like to see more states emulating this model, with a variety of other species and other partners.

I think that an ideal system moving forward would be to have zoos and other professional rearing institutions shift from long-term rearing to protocol development. They could spend several years developing a successful protocol for a particular species, then move the operation into a prison where labor is cheaper and serves the dual function as rehabilitative inmate programming. The zoo could then shift its focus to developing a protocol for a new species. This system would help prison-based facilities be successful, while also solving a funding dilemma for zoos and conservation agencies. One of the problems with long-term rearing operations is that they become increasingly difficult to fund as years go by. Space and money are always at a premium in zoos and it is often easier to fund exciting new projects than continue projects that have been around for a decade or more.

A partnership between zoos and prisons is a natural fit for the rearing of butterflies, and if I could choose a trajectory for my career as an MES graduate, I would hope to facilitate that partnership in many different states. Each new partnership would provide a springboard for new programs in more prisons, helping restore more ecosystems while at the same time providing rehabilitative programming opportunities to more inmates. If I could, I would make helping the synergistic metamorphosis of conservation and incarceration my life’s work.

References

An, Y., S. Wan, X. Zhou, A. A. Subedar, L. L. Wallace, and Y. Luo. 2005. Plant nitrogen concentration, use efficiency, and contents in a tallgrass prairie ecosystem under experimental warming. Global Change Biology 11:1733–1744.

Bachelet, D., B. R. Johnson, S. D. Bridgham, P. V. Dunn, H. E. Anderson, and B. M. Rogers. 2011. Climate change impacts on western Pacific Northwest prairies and savannas. Northwest Science 85:411–429.

Bachelet, D., R. P. Neilson, J. M. Lenihan, and R. J. Drapek. 2001. Climate change effects on vegetation distribution and carbon budget in the United States. Ecosystems 4:164–185.

Barclay, E., M. J. Anderson, H. Wendt, and M. Arnold. 2009. Husbandry manual, Taylor's checkerspot *Euphydryas editha taylori*. Report to the Oregon Zoo, Portland, Oregon.

Bayer, P., R. Pintoff, and D. E. Pozen. 2004. Building criminal capital behind bars: Social learning in juvenile corrections. Discussion paper No. 864, Economic Growth Center, Yale University.

Bazemore, G. 1998. Restorative justice and earned redemption communities, victims, and offender reintegration. American Behavioral Scientist 41:768–813.

Black, S. H., and D. M. Vaughan. 2005. Species profile: *Euphydryas editha taylori*. *in* M. D. Shepherd and D. M. Vaughan, editors. Red List of

Pollinator Insects of North America. The Xerces Society for Invertebrate Conservation, Portland, OR.

Bolton, N., F. V. Smith, K. J. Heskin, and P. A. Banister. 1976. Psychological correlates of long-term imprisonment. British Journal of Criminology 16:38.

Bonney, R., H. Ballard, R. Jordan, E. McCallie, T. Phillips, J. Shirk, and C. C. Wilderman. 2009. Public participation in scientific research: Defining the field and assessing its potential for informal science education. CAISE Inquiry Group Report, Center for Advancement of Informal Science Education, Washington, D.C.

Bowers, M. D. 1981. Unpalatability as a defense strategy of western checkerspot butterflies (*Euphydryas scudder*, Nymphalidae). Evolution 35:367–375.

Brick, P., D. Snow, and S. V. D. Wetering. 2001. Across the great divide: Explorations in collaborative conservation and the American West. Island Press, Washington D. C.

Chappell, C., and R. Crawford. 1997. Native vegetation of the south Puget Sound landscape. *in* P. Dunn and K. Ewing, editors. Ecology and Conservation of the South Puget Sound Prairie Landscape. The Nature Conservancy, Seattle, WA.

Char, P., and P. D. Boersma. 1995. The effects of prairie fragmentation on butterfly species in western Washington. Report to The Nature Conservancy and the U. S. Army, Fort Lewis, University of Washington, Seattle, Washington.

Chen, M. K., and J. M. Shapiro. 2007. Do harsher prison conditions reduce recidivism? A discontinuity-based approach. American Law and Economics Review 9:1–29.

Clampitt, C. A. 1993. Effects of human disturbances on prairies and the regional endemic *Aster curtis* in western Washington. Northwest Science 67:163–169.

Coops, N. C., and R. H. Waring. 2011. Estimating the vulnerability of fifteen tree species under changing climate in Northwest North America. Ecological Modeling 222:2119–2129.

Crawford, R. C., C. Chappell, B. Stephens, C. Soper, and D. Rolph. 1995. Inventory and mapping of endangered native ecosystems of Ft. Lewis. Report to the Environmental and Natural Resources Division, Fort Lewis, Washington. Washington Department of Natural Resources, Natural Hertiage Program and The Nature Conservancy, Olympia, Washington.

Crawford, R., and H. Hall. 1997. Changes in the south Puget prairie landscape. *in* P. V. Dunn and K. Ewing, editors. Ecology and Conservation of the South Puget Sound Prairie Landscape. The Nature Conservancy of Washington, Seattle, Washington.

Crooks, J. A., and M. E. Soule. 2001. Lag times in population explosions of invasive species: Casues and implications. *in* O. T. Sandlund, P. J. Schei, and Å. Viken, editors. Invasive Species and Biodiversity Management. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Dancig-Rosenberg, H., and T. Gal. 2013. Restorative criminal justice. Cardozo Law Review, forthcoming.

Dennehy, C., E. R. Alverson, H. E. Anderson, D. R. Clements, R. Gilbert, and T. N. Kaye. 2011. Management strategies for invasive plants in Pacific Northwest prairies, savannas, and oak woodlands. Northwest Science 85:329–351.

Dornfeld, E. J. 1980. Butterflies of Oregon. Timber Press, Forest Grove, OR.

Dunn, R. R., N. C. Harris, R. K. Colwell, L. P. Koh, and N. S. Sodhi. 2009. The sixth mass coextinction: Are most endangered species parasites and mutualists? Proceedings of the Royal Society B, Biological Sciences 276:3037–3045.

Dunwiddie, P. W., and J. D. Bakker. 2011. The future of restoration and management of prairie-oak ecosystems in the Pacific Northwest. Northwest Science 85:83–92.

Ehrlich, P. R. 1961. Intrinsic barriers to dispersal in checkerspot butterfly. Science 134:108–109.

Ehrlich, P. R. 1965. The population biology of the butterfly, *Euphydryas editha*. II. The Structure of the Jasper Ridge Colony. Evolution 19:327–336.

Ehrlich, P. R., and I. Hanski. 2004. On the wings of checkerspots: A model system for population biology. Oxford University Press, New York, NY.

Ehrlich, P. R., D. D. Murphy, M. C. Singer, C. B. Sherwood, R. R. White, and I. L. Brown. 1980. Extinction, reduction, stability and increase: The responses of checkerspot butterfly (*Euphydryas*) populations to the California drought. Oecologia 46:101–105.

Evans, S., R. Schuller, and E. Augenstein. 1984. A report on *Castilleja levisecta* Greenm. at Rocky Prairie, Thurston County, Washington. Report to The Nature Conservancy, Washington Field Office, Seattle, Washington.

Fimbel, C. 2004. Habitat enhancement for rare butterflies on Fort Lewis prairies. Report to The Nature Conservancy, South Sound Office, Olympia Washington.

Floberg, J., M. Goering, G. Wilhere, C. MacDonald, C. Chappell, C. Rumsey, Z. Ferdana, A. Holt, P. Skidmore, T. Horsman, E. Alverson, C. Tanner, M. Bryer, P. Lachetti, A. Harcombe, B. McDonald, T. Cook, M. Summers, and D. Rolph. 2004. Willamette Valley-PugetTrough-Georgia Basin ecoregional assessment. The Nature Conservancy with support from the Nature Conservancy of Canada, Washington Department of Fish and Wildlife, Washington Department of Natural Resources (Natural Heritage and Nearshore Habitat programs), Oregon State Natural Heritage Information Center and the British Columbia Conservation Data Centre.

Franklin, J. F., and C. T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR.

Gammon, J. 1995. Report on the status of *Castilleja levisecta*. Report to the Washington Natural Heritage Program, Department of Natural Resources, Olympia, Washington

Giles, L. J. 1970. The ecology of the mounds on Mima Prairie with special reference to Douglas-fir invasion. M.S. thesis, University of Washington.

Glaeser, E. L., B. Sacerdote, and J. A. Scheinkman. 1996. Crime and social interactions. The Quarterly Journal of Economics 111:507–548.

Grosboll, D. N. 2004. Captive rearing the endangered mardon skipper (*Polites mardon*) and Taylor's checkerspot (*Euphydryas editha taylori*) butterflies: Initial results (Lepidoptera, Nymphalidae). Proceedings of the Species at Risk Pathways to Recovery Conference, Victoria, B. C.

Grosboll, D. N. 2011. Taylor's checkerspot (*Euphydryas editha taylori*) oviposition habitat selection and larval hostplant use in Washington State. MES thesis. The Evergreen State College.

Hamann, A., and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87:2773–2786.

Hamman, S. T., P. W. Dunwiddie, J. L. Nuckols, and M. McKinley. 2011. Fire as a restoration tool in Pacific Northwest prairies and oak woodlands: Challenges, successes, and future directions. Northwest Science 85:317–328.

Harrison, S., D. D. Murphy, and P. R. Ehrlich. 1988. Distribution of the bay checkerspot butterfly, *Euphydryas editha bayensis*: Evidence for a metapopulation model. The American Naturalist 132:360–382.

Jackson, L. E. 1982. Comparison of phenological patterns in prairie and subalpine meadow communities. Northwest Science 56:316–328.

Karl, T. R., and R. W. Knight. 1998. Secular trends of precipitation amount, frequency, and intensity in the United States. Bulletin of the American Meteorological Society 79:231–241.

Kearns, C. A., D. W. Inouye, and N. M. Waser. 1998. Endangered mutualisms: The conservation of plant-pollinator interactions. Annual Review of Ecology and Systematics 29:83–112.

Klein, J. A., J. Harte, and X.-Q. Zhao. 2004. Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. Ecology Letters 7:1170–1179.

Koh, L. P., R. R. Dunn, N. S. Sodhi, R. K. Colwell, H. C. Proctor, and V. S. Smith. 2004. Species coextinctions and the biodiversity crisis. Science 305:1632–1634.

Lang, F. A. 1961. A study of vegetation change on the gravelly prairies of Pierce and Thurston Counties, Western Washington. M.S. thesis, University of Washington.

Lauber, T. B., R. C. Stedman, D. J. Decker, and B. A. Knuth. 2011. Linking knowledge to action in collaborative conservation. Conservation Biology 25:1186–1194.

Lawrence, B. A., and T. N. Kaye. 2006. Habitat variation throughout the historic range of golden paintbrush, a Pacific Northwest endemic: Implications for restoration. Northwest Science 80:140–152.

Lawrence, B. A., and T. N. Kaye. 2008. Direct and indirect effects of host plants: Implications for reintroduction of an endangered hemiparasitic plant (*Castilleja levisecta*). Madroño 55:151–158.

Lawrence, B. A., and T. N. Kaye. 2011. Reintroduction of *Castilleja levisecta*: Effects of ecological similarity, source population genetics, and habitat quality. Restoration Ecology 19:166–176.

Leopold, E. B., and R. Boyd. 1999. An ecological history of old prairie areas in southwestern Washington. *in* R. Boyd, editor. Indians, Fire and Land in the Pacific Northwest. Oregon State University Press, Corvalis, OR.

LeRoy, C. J., K. Bush, J. Trivett, and B. Gallagher. 2012. The Sustainability in Prisons Project: An overview (2004-12). Gorham Printing, Olympia, WA.

Linders, M. J. 2007. Development of captive rearing and translocation methods for Taylor's checkerspot (*Euphydryas editha taylori*) in south Puget Sound, Washington: 2006-2007 Annual Report. Report to the Washington Department of Fish and Wildlife, Olympia, Washington.

Linders, M. J. 2012. Captive rearing and translocation of Taylor's checkerspot in south Puget Sound: 2011-2012 ACUB Annual Progress Report. Report to the Washington Department of Fish and Wildlife, Olympia, Washington.

Littell, J. S., E. E. Oneil, D. McKenzie, J. A. Hicke, J. A. Lutz, R. A. Norheim, and M. M. Elsner. 2010. Forest ecosystems, disturbance, and climatic change in Washington State, USA. Climatic Change 102:129–158.

MacArthur, R. H. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Mackay, D. A. 1985. Conspecific host discrimination by ovipositing *Euphydryas editha* butterflies: Its nature and its consequences for offspring survivorship. Researches on Population Ecology 27:87–98.

McCallie, E., L. Bell, T. Lohwater, J. H. Falk, J. L. Lehr, B. V. Lewenstein, C. Heedham, and B. Wiehe. 2009. Many experts, many audiences: Public engagement with science and informal science education. A CAISE Inquiry Group Report, Center for Advancement of Informal Science Education, Washington, D.C.

McLaughlin, J. F., J. J. Hellmann, C. L. Boggs, and P. R. Ehrlich. 2002. Climate change hastens population extinctions. Proceedings of the National Academy of Sciences 99:6070–6074.

del Moral, R., and D. C. Deardorff. 1976. Vegetation of the Mima Mounds, Washington State. Ecology 57:520–530.

Morris, W. G. 1934. Forest fires in western Washington and western Oregon. Oregon Historical Quarterly 35:313–339.

Mote, P. W., and E. P. Salathé. 2010. Future climate in the Pacific Northwest. Climatic Change 102:29–50.

Nadkarni, N. M. 2004. Not preaching to the choir: Communicating the importance of forest conservation to nontraditional audiences. Conservation Biology 18:602–606.

Nadkarni, N. M. 2006. The moss-in-prison project: Disseminating science beyond academia. Frontiers in Ecology and the Environment 4:442–443.

Nadkarni, N. M. 2007. Ecological outreach to faith- based communities. Frontiers in Ecology and the Environment 5:332.

Nisbet, J. 2009. The Collector: David Douglas and the Natural History of the Northwest. Sasquatch Books, Seattle, WA.

Norton, H. H. 1979. The association between anthropogenic prairies and important food plants in western Washington. Northwest Anthropological Research Notes 13:175–200.

Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. Report to the U. S. Department of the Interior, National Biological Service, Washington D. C.

Phelps, M. S. 2011. Rehabilitation in the punitive era: The gap between rhetoric and reality in U.S. prison programs. Law & Society Review 45:33–68.

Pyle, R. M. 2002. The Butterflies of Cascadia: A Field Guide to All the Species of Washington, Oregon, and Surrounding Territories. Seattle Audubon Society, Seattle, WA.

Pyle, R. M., and S. A. Society. 1974. Watching Washington Butterflies: An Interpretive Guide to the State’s 134 species, Including Most of the Butterflies of Oregon, Idaho, and British Columbia. Seattle Audubon Society, Seattle, WA

Quammen, D. 2012. The Song Of The Dodo: Island Biogeography in an Age of Extinctions. Scribner Island Press, New York, NY

Rehfeldt, G. E., N. L. Crookston, M. V. Warwell, and J. S. Evans. 2006. Empirical analyses of plant-climate relationships for the western United States. International Journal of Plant Sciences 167:1123–1150.

Rezende, E. L., J. E. Lavabre, P. R. Guimarães, P. Jordano, and J. Bascompte. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. Nature 448:925–928.

Ross, D. 2003. First year (2003) cencus of the Carwell Hill population of Taylor's checkerspot (*Euphydryas editha taylori*) in Benton County, Oregon. Report to the Xerces Society, Corvallis, Oregon.

Rustad, L., J. Campbell, G. Marion, R. Norby, M. Mitchell, A. Hartley, J. Cornelissen, J. Gurevitch, and GCTE-NEWS. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543–562.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A., S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. Mccauley, P. O'neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32:305–332.

Schultz, C. B., E. Henry, A. Carleton, T. Hicks, R. Thomas, A. Potter, M. Collins, M. Linders, C. Fimbel, S. Black, H. E. Anderson, G. Diehl, S. Hamman, R. Gilbert, J. Foster, D. Hays, D. Wilderman, R. Davenport, E. Steel, N. Page, P. L. Lilley, J. Heron, N. Kroeker, C. Webb, and B. Reader. 2011.

Conservation of prairie-oak butterflies in Oregon, Washington, and British Columbia. Northwest Science 85:361–388.

Severns, P. M., and D. Grosboll. 2011. Patterns of reproduction in four Washington State populations of Taylor's checkerspot (*Euphydryas editha taylori*) during the spring of 2010. Report to The Nature Conservancy, Olympia, Washington.

Severns, P. M., and A. D. Warren. 2008. Selectively eliminating and conserving exotic plants to save an endangered butterfly from local extinction. Animal Conservation 11:476–483.

Shafer, S. L., P. J. Bartlein, and R. S. Thompson. 2001. Potential changes in the distributions of western North America tree and shrub taxa under future climate scenarios. Ecosystems 4:200–215.

Shaver, G. R., J. Canadell, F. S. Chapin, J. Gurevitch, J. Harte, G. Henry, P. Ineson, S. Jonasson, J. Melilo, L. Pitelka, and L. Rustad. 2000. Global warming and terrestrial ecosystems: A conceptual framework for analysis. BioScience 50:871–882.

Sheehan, M., and N. Sprague. 1984. Report on the status of Castilleja levisecta Greenm. Report to The Nature Conservancy, Seattle, Washington.

Shepard, J., and C. Guppy. 2011. Butterflies of British Columbia: Including Western Alberta, Southern Yukon, the Alaska Panhandle, Washington, Northern Oregon, Northern Idaho, and Northwestern Montana. UBC Press, Vancouver B. C.

Shepard, J. H. 2000. Status report on Taylor's checkerspot *Euphydryas editha taylori* (Edwards) (Lepidoptera: Nymphalidae) in British Columbia. Report to the Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario.

Singer, M. C. 1972. Complex components of habitat suitability within a butterfly colony. Science 176:75–77.

Singer, M. C. 1982. Quantification of host preference by manipulation of oviposition behavior in the butterfly *Euphydryas editha*. Oecologia 52:224–229.

Singer, M. C., and P. R. Ehrlich. 1979. Population dynamics of the checkerspot butterfly *Euphydryas editha*. Fortschritte der Zoologie 25:53–60.

Singer, M. C., and J. R. Lee. 2000. Discrimination within and between host species by a butterfly: Implications for design of preference experiments. Ecology Letters 3:101–105.

Singer, M. C., D. Ng, and R. A. Moore. 1991. Genetic variation in oviposition preference between butterfly populations. Journal of Insect Behavior 4:531–535.

Singer, M. C., D. Ng, and C. D. Thomas. 1988. Heritability of oviposition preference and its relationship to offspring performance within a single insect population. Evolution 42:977-985.

Singer, M. C., D. Vasco, C. Parmesan, C. D. Thomas, and D. Ng. 1992. Distinguishing between "preference" and "motivation" in food choice: An example from insect oviposition. Animal Behaviour 44, Part 3:463–471.

Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller. 2007. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change, 2007. Cambridge University Press, New York, NY.

Stanley, A. G., T. N. Kaye, and P. W. Dunwiddie. 2008. Regional strategies for restoring invaded prairies. Native Plants Journal 9:247 –254.

Stinson, D. W. 2005. Draft status report for the Mazama pocket gopher, streaked horned lark, and Taylor’s checkerspot. Report to the Washington Department of Fish and Wildlife, Olympia, Washington.

Storm, L., and D. Shebitz. 2006. Evaluating the purpose, extent, and ecological restoration applications of indigenous burning practices in southwestern Washington. Ecological Restoration 24:256–268.

Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland responses to changing climate. Science 315:640–642.

Tveten, R. 1997. Fire effects on prairie vegetation, Fort Lewis, Washington. *in* P. V. Dunn and K. Ewing, editors. The Ecology and Conservation of the South Puget Sound Landscape. The Nature Conservancy of Washington, Seattle, WA.

de Valpine, P., and J. Harte. 2001. Plant responses to experimental warming in a montane meadow. Ecology 82:637–648.

Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V. Callaghan, A. B. Carroll, H. E. Epstein, I. S. Jónsdóttir, J. A. Klein, B. Magnússon, U. Molau, S. F.

Oberbauer, S. P. Rewa, C. H. Robinson, G. R. Shaver, K. N. Suding, C. C. Thompson, A. Tolvanen, Ø. Totland, P. L. Turner, C. E. Tweedie, P. J. Webber, and P. A. Wookey. 2006. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences 103:1342–1346.

Weber, S. R., 2012. Environmental education in prison: A comparison of teaching methods and their influence in inmate attitudes and knowledge of environmental topics. MES thesis. The Evergreen State College.

Weiss, S. B. 1999. Cars, cows, and checkerspot butterflies: Nitrogen deposition and management of nutrient-poor grasslands for a threatened species. Conservation Biology 13:1476–1486.

Weiss, S. B., D. D. Murphy, and R. R. White. 1988. Sun, slope, and butterflies: Topographic determinants of habitat quality for *Euphydryas Editha*. Ecology 69:1486–1496.

Wentworth, J. B. 2001. The demography and population dynamics of Castilleja levisecta, a federally threatened perennial of Puget Sound grasslands. *in* R. S. Reichard, P. Dunwiddie, J. Gamon, A. Kruckeberg, and D. Salstrom, editors. Conservation of Washington's Native Plants and Ecosystems. Washington Native Plant Society, Seattle, Washington

Wenzel, M., T. G. Okimoto, N. T. Feather, and M. J. Platow. 2008. Retributive and restorative justice. Law and Human Behavior 32:375–389.

Western, B., J. R. Kling, and D. F. Weiman. 2001. The labor market consequences of incarceration. Crime & Delinquency 47:410–427.

Wold, E. N., J. E. Jancaitis, T. H. Taylor, and D. M. Steeck. 2011. Restoration of agricultural fields to diverse wet prairie plant communities in the Willamette Valley, Oregon. Northwest Science 85:269–287.

Zavaleta, E. S., M. R. Shaw, N. R. Chiariello, H. A. Mooney, and C. B. Field. 2003. Additive effects of simulated climate changes, elevated CO2, and nitrogen deposition on grassland diversity. Proceedings of the National Academy of Sciences 100:7650–765