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CONSERVATION ISSUES

Intertwined Fates: Opportunities and Challenges in the Linked Recovery of Two Rare Species

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ABSTRACT: Rare species recovery presents several challenges for conservation managers, particularly when listed species interact with one another. We present a case study involving two such species: golden paintbrush (*Castilleja levisecta*) and Taylor's checkerspot butterfly (*Euphydryas editha taylori*), both of which occur in lowland prairies in the Puget Sound region and are federally protected (threatened and endangered, respectively). These two species occupy some of the same sites, and golden paintbrush likely historically served as a larval food plant for Taylor's checkerspot. Managers working to recover these species have encountered a number of challenges and opportunities—recovery efforts for one species may have no effect, positive effects, or negative effects on the other. Furthermore, sometimes rapid recovery actions are necessary on shorter time scales than those at which research typically occurs, and must proceed in spite of significant knowledge gaps. Here we share how our growing understanding of the complex ecology of these species has given rise to large-scale management questions and conflicts, and outline the strategies we are using to navigate these challenges. Our approach has included convening periodic workshops with experts on both species; designing and implementing research studies to fill knowledge gaps about the two species' relationship; and identifying "no regrets" actions that can be taken to benefit one or both species with minimal risk in the face of uncertainty. While the details of this case study are highly specific, the lessons can be applied to other systems with interacting listed species.

Index terms: Castilleja levisecta, *Euphydryas editha taylori*, rare species, synergistic recovery

INTRODUCTION

The recovery of rare species presents challenges for government agencies, land managers, and conservation organizations worldwide. Knowing when, where, and how to begin recovery can be difficult, as fundamental aspects of the biology, ecology, and interactions among rare organisms are often unknown or absent from recovery plans (Tear et al. 1995; Boersma et al. 2001; Soulé et al. 2005). In addition, key factors contributing to their decline or scarcity are often unknown (Raphael and Molina 2007), yet understanding them may be critical to preventing continued decline, or aid in mapping out effective recovery actions. These information gaps can lead to tension among parties engaged in recovery actions. For example, agencies that oversee the recovery process, or personnel who manage lands where vulnerable populations persist, may want to see rapid and tangible progress in species recovery, yet those responsible for implementing recovery actions may be unsure of the relative importance of the many possible actions that could be taken or how to prioritize among them. Furthermore, researchers studying the organism may be particularly aware of knowledge gaps about the species and its ecology, yet addressing those gaps may proceed at a pace that lags behind on-the-ground actions. The net result of these tensions can be considerable uncertainty about how to proceed, and may lead to inaction.

These challenges may be compounded when multiple rare species share habitat or interact with one another, as actions taken to recover one species may or may not benefit the other species (Simberloff 1998). Antagonistic interactions between rare species can lead to management conflicts; for example, endangered animals may compete for nest sites or foraging areas with each other (Lee et al. 2007; Oro et al. 2009), or may prey on one another (Gumm et al. 2011; Chadés et al. 2012). Occasionally, the species interact intimately, necessitating extensive, close coordination among researchers and managers involved in recovery efforts. Such coordination may be straightforward where relationships are well-established, the species share similar threats, or where they may have an obligate relationship, such as with Fender's blue butterfly (*Icaricia icarioides fenderi* Macy) and its host plant, Kincaid's lupine (*Lupinus oreganus* var. *kincaidii* C.P. Sm.) (Schultz 2001). However, coordination can be considerably more complicated when species can interact strongly but do so facultatively, rather than obligately.

In this paper, we explore how species recovery efforts, land management, and research have addressed these issues using a case study of two protected species with poorly understood yet intertwined fates—Taylor's checkerspot butterfly (*Euphydryas editha taylori* W.H. Edwards; Nymphalidae) and golden paintbrush (*Castilleja levisecta*

Greenm.; Orobanchaceae). Until recently, efforts to restore viable populations of Taylor's checkerspot and golden paintbrush proceeded along parallel but largely independent trajectories. However, as these efforts evolved and our understanding of the biology of each species increased, we began to recognize the potential interactions between them. These interactions have affected recovery both in terms of space (e.g., where recovery was occurring on the ground) and of the actions themselves, as actions taken for one species were deemed likely to strongly influence outcomes for the other. Here, we describe the process by which scientists and conservation partners have begun to identify linkages between these species and to characterize the risks and opportunities associated with their joint recovery. We begin by reviewing each species' history and ecology, outlining actions that improve their status and move them towards recovery. Based on this case study, we highlight insights and implications relevant to those involved in the recovery of other interacting listed species.

BACKGROUND

The two species that are the focus of this case study—Taylor's checkerspot and golden paintbrush (Figure 1)—both occurred historically in lowland prairies in the Pacific Northwest. These habitats all occur in a Mediterranean-type climate characterized by relatively mild, wet winters, and warm, dry summers, but they are distributed across a broad range of sites, from shallow, stony soils, coastal bluffs and rocky balds, to relatively rich, deep-soil prairies. Only a small fraction of these communities exist today, the vast majority having been converted to agriculture, developed, or overgrown by forest (Dunwiddie and Bakker 2011). Most of the remnants that persist are degraded and highly fragmented. However, precise historical occurrence data are sparse for both species, so there is considerable uncertainty regarding where they historically occurred within this continuum of conditions.

The detailed information about the ecology of each species presented in the following sections provides important background, as many of the synergies and conflicts between the two recovery efforts have emerged from the minutia of each species'

Figure 1. Taylor's checkerspot on golden paintbrush (Photo: Nathan Haan).

natural history and biotic interactions. In many ways, this is a case study of ways in which details about each species give rise to complex issues that influence the fates of both species.

Golden Paintbrush

Golden paintbrush occurred historically from coastal islands in southern British Columbia to the Willamette Valley in Oregon. Extensive loss of prairies across the region has dramatically reduced potential habitat for the species. Only about a dozen wild populations remain, primarily in Washington; it was extirpated from Oregon in 1938.

Recovery efforts began in the late 1990s when golden paintbrush was designated as a threatened species under the Endangered Species Act (Federal Register 1997). The US Fish and Wildlife Service has provided extensive funding both to establish new populations and to augment existing populations, some of which had declined to <100 plants. These efforts are yielding promising results, with several new populations—some numbering in the tens of thousands of plants—successfully established in prairies spanning the historical range of the species (Arnett 2014).

Most extant populations occur in relatively unproductive sites close to the coast (Chappell and Caplow 2004), and early recovery efforts focused on sites with similar soils. However, new, large populations of extremely vigorous plants have recently been established in former agricultural sites with deep soils (Delvin 2013). Deep-soil prairies, which at one time were extensive in both Oregon and Washington, were among the first to be transformed by European settlers due to their suitability for agriculture. Based on our observations of these new populations, we hypothesize that the species may have thrived in more productive sites and that the extant natural populations are not representative of the species' ecological amplitude. Such occurrences are not unprecedented; Hanski et al. (2004:271) noted "exclusion from more productive areas is a common situation for many threatened species, which persist as relict populations in relatively low-quality habitats."

Golden paintbrush is a short-lived hemiparasite that can attach to the roots of various other species. These host plants provide the paintbrush with nutrients and water (Heckard 1962).

Golden paintbrush recovery has proceeded largely on two fronts: habitat restoration and management, and establishment of new populations. Habitat restoration and management efforts include prescribed fire, removal of invading trees and shrubs, and chemical treatment of herbaceous nonnative invasive species. These are standard management practices for Puget prairies in general, so they occur with or without explicit intention to recover golden paintbrush.

The second recovery strategy is establishment of new golden paintbrush populations. Efforts initially focused on outplanting nursery-grown plugs into native prairies. Survival and regeneration varied widely, even within a single site, leading to conclusions that establishment strongly depended on finding suitable microsites (Dunwiddie and Martin 2016). However, recent research demonstrated that golden paintbrush can be directly seeded simultaneously with other native prairie species in abandoned agricultural fields (Delvin 2013). Several of the largest current populations of golden paintbrush were established by seeding directly into prepared planting sites, which only became possible as we developed large seed production beds in nurseries.

Early research on golden paintbrush focused on relationships with host plants (Lawrence and Kaye 2008), fire (Dunwiddie et al. 2001), demography (Gamon et al. 2001), genetics (Godt et al. 2005), and restoration (Pearson and Dunwiddie 2006). Current research foci include the effects of host plant identity on performance, quantification of the resources golden paintbrush acquires from its host plants, its potential role in structuring plant communities, and its interactions with other trophic levels.

Taylor's Checkerspot

Taylor's checkerspot is a subspecies of Edith's checkerspot (*Euphydryas editha* Boisduval). The range of Taylor's checkerspot is largely sympatric with that of golden paintbrush, although a few populations of the butterfly occur on balds and in montane habitats at higher elevations (Stinson 2005). Like the paintbrush, Taylor's checkerspot has largely disappeared from British Columbia and Oregon, but is still found at multiple sites in Washington. Populations—including several that numbered in the thousands—have been in decline for decades, and many have disappeared entirely in the last 15 years. Causes likely include loss and degradation of habitat, stochastic loss of small and isolated populations, and loss of metapopulation dynamics as individual populations disappeared. It is currently known to occur on only ten sites. The largest population, and the only naturally occurring one left in the lowland prairies of western Washington, occupies a portion of the large ordnance, live-fire Artillery Impact Area on Joint Base Lewis-McChord (JBLM) near Olympia; the site is subjected to frequent low severity fires as a result of the munitions training.

Taylor's checkerspot became a federal candidate under the US Endangered Species Act in 2001, and was listed as endangered in 2013, so no recovery plan has yet been developed for this species (http://www.fws.gov/oregonfwo/Species/Data/Taylors-Checkerspot/). Because it occurs on a key military training installation, the US Department of Defense has provided substantial funding to restore Taylor's checkerspot at off-base sites and thereby minimize the conservation burden on JBLM's training lands. Interestingly, there is no record of golden paintbrush from this site. Efforts to reintroduce the butterfly to historical sites in Washington were initiated in 2006.

Relatively little formal research has been conducted with Taylor's checkerspot to date, although other subspecies of Edith's checkerspot have been the subject of extensive study, particularly in California (Ehrlich and Hanski 2004). Our knowledge of the biology and ecology of Taylor's checkerspot has been inferred from these extensive studies on other subspecies and refined by direct observations of extant populations. Checkerspots have been a model system for population studies because their life histories are notoriously complex. For example, traits associated

with host plant usage vary widely among subspecies and populations, and subspecies occur in metapopulations; individual populations may grow, decline, or be extirpated over relatively short time periods (Ehrlich and Hanski 2004; Singer and McBride 2009). These ecological complexities make the species especially challenging to conservationists charged with recovery and management of individual populations.

Taylor's checkerspot is single-brooded throughout its range, and can occur at relatively high densities in forb-rich grasslands, where it uses a variety of larval host and nectar species for food (Stinson 2005). It is a year-round resident and has relatively limited dispersal capabilities. Adults typically fly in late April to early June in the Puget Sound lowlands, and often aggregate in dense colonies to mate and lay eggs.

After mating, females lay eggs in clusters at the base of host plants or on the undersides of leaves. Primary oviposition plants of extant populations are lanceleaf plantain (*Plantago lanceolata* L.) and harsh paintbrush (*Castilleja hispida* Benth.), although females will also oviposit on *Veronica* spp. and occasionally other related taxa. Oviposition preference is largely genetically inherited (Singer et al. 1991), although a female may oviposit on more than one host species. At present, plantain is the primary oviposition host used by several natural populations of Taylor's checkerspot. Plantain was first introduced to Washington in the 1800s, suggesting that butterfly populations opportunistically expanded or shifted their diets to include plantain. Host switching is not uncommon in checkerspots, and in fact, many populations have altered their diets to include plantain (Bowers et al. 1992; Ehrlich and Hanski 2004). Use of nonnative species is also more widespread than just by checkerspots—a third of the California butterfly fauna include nonnatives in their suite of host plants (Graves and Shapiro 2003), and endangered species in other taxonomic groups also benefit from nonnative species in some circumstances (e.g., Chiba 2010).

Eggs hatch within a few weeks, and larvae must grow quickly before the host plants on which they feed senesce during summer droughts typical of the region. Young larvae (early instars) are too small to disperse more than about 10 cm from the plant where they hatched and, thus, are at the mercy of the female's oviposition choice (Ehrlich and Hanski 2004). After several instars, the larvae enter diapause (dormancy) in midsummer as nearly mature larvae, reemerging in late winter to complete their final larval instar before pupating and emerging as adults (Stinson 2005). Older, late instar larvae are able to move from plant to plant and may feed on a larger suite of plant species, including the native annuals blue-eyed Mary (*Collinsia parviflora* Lindl., *C. grandiflora* Douglas ex Lindl.) and seablush (*Plectritis congesta* (Lindl.) DC.). Completion of the checkerspot life cycle typically requires one year.

The current strategies being used to recover Taylor's checkerspot are the same as for golden paintbrush: habitat restoration and management, and establishment of new populations. In South Puget Sound, the restoration objective has been to return degraded grasslands, typically dominated by European pasture grasses and shrubs, to a forb-rich condition containing dense and diverse larval host and nectar plants in a low, open vegetation structure. An open vegetation structure provides adult and larval basking sites and access to oviposition locations, while a diversity of host and nectar species ensures sufficient food at all life stages regardless of weather and microsite conditions. Restoration techniques include controlling invasive species, manipulating vegetation structure using mowing, prescribed fires, judicious use of herbicides, and planting and seeding of forbs known to be important in the checkerspot life cycle (larval host plants, nectar plants, basking sites), together with a matrix of native grasses.

Establishment of new populations is being accomplished via captive rearing and reintroduction to historically occupied prairies. This reintroduction effort includes the development of captive rearing and mating methods (Barclay et al. 2009), and of release and monitoring techniques (Linders and Lewis 2013). Since the first releases of Taylor's checkerspot in 2006, postdiapause larvae have been released at five sites, with three sites receiving two or more sequential releases (Linders and Lewis 2013). Three years after its last release, one site maintains a population in the thousands (Linders et al. 2014).

Formal research to date on Taylor's checkerspot has focused mostly on the adult stage of the life cycle, including studies of mating and dispersal behavior (Bennett et al. 2012, 2013), female movement behavior (Severns and Breed 2014), oviposition habitat (Grosboll 2011), oviposition preference (Aubrey 2013), and microclimate effects on habitat use (Bennett et al. 2014). Ongoing research is focused on habitat preferences of adult butterflies, and on interactions between larvae and host plants. Other research needs include the effects of spatial configuration of host plants on oviposition and larval feeding, effects of timing and severity of fire on diapausing larvae, and effects of herbicide and other land management practices on larvae.

POTENTIAL FOR JOINT RECOVERY

Evidence for Ecological Links between Taylor's Checkerspot and Golden Paintbrush

Perhaps the strongest evidence of an ecological link between Taylor's checkerspot and golden paintbrush comes from a site in south Puget Sound where Taylor's checkerspots were known to exist until 1997. This site is the only extant wild population of golden paintbrush in south Puget Sound, and one of the largest (5–10,000 flowering plants). Several noteworthy observations were made there in 1983 during a detailed study of golden paintbrush that suggest a direct connection between these species. In mid-May, a pair of checkerspots was observed "mating on *C. levisecta,*" and an individual checkerspot was observed "either resting or laying eggs" on *C. levisecta* (Evans et al. 1984, unpub. data). Further observations were made of clusters of caterpillars in early June "virtually defoliating" a golden paintbrush plant (Evans et al. 1984, unpub. data). Two additional, similar larval clusters were observed later in June, one on golden paintbrush and one

on harsh paintbrush, which also occurred on the site at that time (Evans et al. 1984, unpub. data). Based on the authors' description, the larvae were identified by the lepidopterist R.M. Pyle as "almost without doubt the larva[e] of Edith's checkerspot butterfly." Taylor's checkerspot is the only common checkerspot in the South Puget Sound prairies.

Other lines of evidence suggest these two species were ecologically linked in the past. For example, numerous checkerspot occurrences were documented in the vicinity of Victoria, British Columbia, through the early 1960s, including at least two locations where golden paintbrush also occurred. Nearby in the San Juan Islands, both species co-occurred as recently as 1979 on one island (A. Potter, Conservation Biologist, Washington Department of Fish and Wildlife, pers. comm. 2013). Thus, it appears that these species were formerly sympatric, though their declines during the 20th century have eliminated overlapping populations and precluded present day interactions.

Recent studies are providing evidence that Taylor's checkerspot is able to use golden paintbrush. During captive rearing trials at the Oregon Zoo in 2004, prediapause larvae were successfully reared on foliage from golden paintbrush (M.J. Andersen, Oregon Zoo staff, unpubl. data). More recently, Aubrey (2013) conducted an oviposition preference study using gravid Taylor's checkerspots in captivity, and demonstrated that either species of *Castilleja* was preferred over plantain. Finally, during spring 2013, we released postdiapause larvae on golden paintbrush in the field and documented their survival and activities until pupation. We found that they remained near and fed on golden paintbrush at rates similar to larvae released on plantain, and observed several adult checkerspots in the plots, most likely originating from the larvae we released. Thus, it appears golden paintbrush is a suitable host plant at least for postdiapause larvae. It is still unknown whether females will select it for oviposition in natural settings, and whether it is phenologically and chemically suitable for prediapause larvae.

Complications of Joint Recovery

When rare and protected species interact, it can lead to unique situations that require creative solutions, both ecologically and organizationally. Some interactions lead to seemingly inescapable tradeoffs: for example, the endangered Andouin's gull (*Larus andouinii* Payr.) competes for nest space with other rare seabirds and decreases diversity at nesting habitats where it is present (Oro et al. 2009). Other antagonistic interactions between protected species can be diffused by human intervention. For example, Gumm et al. (2011) describe recent interactions between two endangered fish species; as habitat became more restricted, one began to prey on the eggs of the other, contributing to its decline. By expanding and restoring breeding habitats, managers were able to decrease egg predation rates and populations rebounded (Gumm et al. 2011). Finally, where a plant and herbivore interact strongly with sublethal effects for the plant (e.g., Kincaid's lupine and Fender's blue butterfly), habitat improvements included vigorous seeding of host plants (Schultz 2001).

In contrast to some of these examples, interactions between golden paintbrush and Taylor's checkerspot remain poorly understood, and the potential conflicts and synergies between these species are complex, multifaceted, and in some cases are still unknown. They require clarification, and doing so will require cooperation and compromise within and among organizations involved in their recovery. In particular, progress has been impeded by uncertainty about the relative suitability of various checkerspot host plants and the ways their suitability could vary with soils and other abiotic habitat characteristics. We are also working to clarify issues of hybridization between the two paintbrush species. Finally, we are working to align habitat management objectives for Taylor's checkerspot and golden paintbrush so they complement, rather than conflict, with one another.

Various larval food plants have been used in plantings to enhance habitat for recovering Taylor's checkerspots. However, the relative value of the various species to larval performance in Taylor's checkerspot is a complicated issue. Even though it is a nonnative species, lanceleaf plantain is included in habitat plantings because it is the primary host plant known to be used by extant checkerspot populations in the region, it is used by all life stages, and it is more likely to resist desiccation during the larval feeding period than most of the native hosts. However, it is also susceptible to a fungal pathogen that can significantly reduce the abundance of green plant material in early winter when larvae emerge from diapause.

In addition to plantain, harsh paintbrush is also planted extensively and is heavily used for oviposition where it occurs on south Puget Sound lowland sites. However, anecdotal observations suggest prediapause larval starvation due to host desiccation in early summer may be cause for concern (M. Linders, N. Haan, pers. obs.). Plantain is utilized by checkerspots more often than harsh paintbrush, but it remains an open question whether this is because it is a preferred host, or whether butterflies simply encounter it more often since it is more abundant than native hosts. In addition to plantain and harsh paintbrush, restoration plantings have emphasized other food species, such as sea blush and blue-eyed Mary. These annual species germinate in fall and grow slowly through the winter, providing food to larvae emerging from diapause. However, they typically desiccate shortly after the adult flight season, making them unsuitable for prediapause larvae.

Larval starvation is a significant source of mortality for Edith's checkerspot, accounting for over 90% of larval mortality in some California populations (Weiss et al. 1988; Erhlich and Hanski 2004). Prediapause larvae race to consume their food plants before the summer drought; if the plants desiccate before larvae are big enough to survive diapause, the larvae starve. Several ecological alternatives may provide feasible pathways for Taylor's checkerspot larvae facing the onset of summer drought. Historically, larvae feeding on harsh paintbrush may have experienced high mortality on sites and in years when weather conditions caused plants to desiccate early. Plantain, which resists drought better than the native

hosts, may have been more available to larvae under these conditions, triggering a host shift. Another related possibility is that historically, one or both species of paintbrush occurred across a wider range of site conditions than at present. Of particular note, we have found that golden paintbrush sown in deeper soiled sites emerge earlier, grow larger, and remain greener longer than those growing on the excessively well-drained sites currently in conservation status. Furthermore, golden paintbrush establishes more successfully and grows larger than harsh paintbrush when seeded together in the deep soil sites. This suggests these deep-soil sites may be able to not only support vigorous populations of golden paintbrush, but that these sites also may be able to support more robust and stable checkerspot populations than the native prairie remnants where checkerspot restoration currently is taking place. The vigor and size of golden paintbrush populations that have recently been restored to these sites, which now exceed 100,000 flowering plants, largely negates any risk that feeding by large numbers of checkerspot larvae could compromise recovery of golden paintbrush.

Remnant populations of rare species are frequently found persisting in ecologically marginal sites (Falk et al. 1996; Erhlich and Hanski 2004), and caution should be used when characterizing suitable habitat based on a few remaining occurrences of a rare species. Both golden paintbrush and Taylor's checkerspot may be examples of this, which raises the possibility that recovery efforts for both species may be focused on sites that are less than optimal, with consequent implications for our understanding of the species' relationships.

Another unusual challenge occurs because golden paintbrush and harsh paintbrush hybridize with one another (Kaye and Blakeley-Smith 2008). This became apparent when both paintbrush species were planted at high densities in close proximity to one another, and apparent hybrids with intermediate morphological features began to appear. Managers working on recovery of golden paintbrush are understandably concerned because of the potential to compromise golden paintbrush recovery. Similarly, biologists working on recovery of Taylor's checkerspot grew concerned about loss of recovery potential as more and more sites were planted with golden paintbrush. Therefore, a compromise was reached: new plantings of either paintbrush species would occur at least 200 m from populations of the other species. This is not a preferred solution as this spatial separation is not ecologically determined and puts spatial restrictions on recovery efforts for both golden paintbrush and Taylor's checkerspot. However, if, as we expect, golden paintbrush is verified as a suitable host for Taylor's checkerspot, coordinated actions that promote the recovery of both species may proceed in many areas that provide high quality habitat for both taxa.

Concerns have also been raised about the potential impacts on Taylor's checkerspot of various land management actions to sustain golden paintbrush populations and improve native prairie vegetation, such as the use of prescribed fire and herbicides. Similarly, there are concerns that the introduction of checkerspots to sites will present both practical and legal impediments to on-going management of golden paintbrush populations and habitat. Perhaps the most unusual collision of management objectives has been the effort to control nonnative species in the prairies, while simultaneously spreading the nonnative plantain as a larval food plant for checkerspots.

Joint Recovery: Moving Forward

The increasing body of evidence suggesting ecological linkages between Taylor's checkerspot and golden paintbrush is redefining discussions and promoting actions relating to recovery of both species. Recovery actions for both taxa are proceeding rapidly, spurred on by federal listing of both species, availability of recovery funding, and the precarious status of the few remaining populations. However, the differential timing of the federal listing of the two species has contributed to the complications in coordinating their recovery. For example, the golden paintbrush recovery plan (USFWS 2000) helped galvanize extensive research and recovery action on this species, but made no mention of potential ecological interactions of this species with Taylor's checkerspot. Thus, it is critical that as the recovery plan for the butterfly is developed, it directly addresses both the synergies and conflicts that are presented by these interactions so that recovery of both species can proceed expeditiously. In addition, it is imperative that it be flexible to accommodate new ecological understanding.

Questions remain regarding the recovery of both species. Will female checkerspots lay eggs on golden paintbrush in the wild? Might this be affected by the identity of the host plant(s) that golden paintbrush is parasitizing? To what extent will golden paintbrush provide suitable resources for pre- and post-diapause larval feeding? Do larval host plants vary in effectiveness among microsites? How will management activities such as prescribed burning, which is intended to promote golden paintbrush, affect Taylor's checkerspot larvae that are in diapause? It is important but difficult to identify which questions are essential to answer, and whether they must be answered before moving forward with joint recovery of these species at particular sites.

Balancing these research needs with the necessity to move ahead expeditiously on recovery actions for both species is a dilemma. Research must be sufficiently rigorous to enable managers to conduct recovery actions with confidence, yet funding is often inadequate to support research at the intensity and duration needed to adequately address the questions. It is difficult to obtain quick and definitive answers to many of these questions due to the complex interaction of variables that characterize field studies (e.g., annual weather patterns, metapopulation dynamics, fire behavior, species interactions, microsites), and because of challenges working with species that are cryptic or undetectable during significant parts of their life cycle. Yet, it would be unwise to delay recovery actions until all questions are answered. Like research, restoration requires many years of intensive effort; site preparation, planting, and maturation to suitable habitat take time. Restoration actions may also be difficult to reverse if, for example, host species are established that are later deemed unsuitable.

INSIGHTS AND IMPLICATIONS

In light of these challenges, we have taken three steps to overcome obstacles and proceed with recovery of both species quickly, thoughtfully, and in ways that minimize conflicts and capitalize on the potential synergies of joint recovery. These steps are: (1) Convening expert workshops to identify areas of overlap, conflict, and opportunity, (2) Prioritization, design, and implementation of research studies that provide guidance on key questions, and (3) Identification and implementation of "no regrets" actions that can occur quickly and are unlikely to have adverse effects for either species.

We organized expert workshops, drawing together scientists and managers from government agencies, nonprofits, and universities. We encouraged participants to identify and discuss particularly difficult issues, for example, areas in which recovery efforts for the two species have conflicted in the past or might in the future, or elements of an organism's ecology for which there is no consensus. We then asked attendees to rate these issues in terms of the risks to potential joint recovery actions. This allowed us to highlight the issues most in need of attention, as there were wide differences of opinion about them. Having identified these issues, we were able to clarify misunderstandings (e.g., personnel working on recovery of golden paintbrush may lack up-to-date knowledge of Taylor's checkerspot and vice versa) and to identify important knowledge gaps (e.g., do paintbrush hybrids produce viable seeds?). Convening these workshops brought us closer to a shared vision of mutual progress.

On a practical level, these workshops also allowed us to coordinate management activities for the two species so they complement one another. For example, controlled burns can be planned collaboratively such that they avoid areas where concentrations of diapausing larvae are likely to be high, and can be conducted in areas that are being prepared for release of captive-reared larvae in subsequent years. Similarly, the spatial extent of fires, as well as the conditions under which burns are conducted, can be adjusted. Finally, as noted above, we have adopted a 200-m buffer between plantings of golden paintbrush and harsh paintbrush and have mapped out and designated areas of various preserves for each species.

Another important outcome of these workshops was the development and implementation of a shared research agenda. Even though complete consensus was not reached regarding the relative importance of various research needs, we identified areas in which subgroups could collaborate to advance our collective research agenda. For example, one recently identified goal is to determine experimentally whether golden paintbrush is a suitable host for prediapause larvae in field settings. If so, the rewards could be substantial—checkerspot habitat enhancements could include golden paintbrush instead of the more common harsh paintbrush at some sites, and additional checkerspot populations could be founded in the extensive golden paintbrush populations that have been sown on deep-soil sites in recent years. To address this goal, we are experimentally releasing checkerspot eggs onto plots containing golden paintbrush, harsh paintbrush, and plantain, monitoring larval performance on each host, and evaluating whether phenological synchrony between hosts and larvae differs among soil and physical environments. We anticipate that the relative suitability of these three species will depend on their environment—for example, we suspect plantain may be the most phenologically suitable host in dry areas with well-drained soils, while golden paintbrush could be more suitable in mesic areas with deeper soils. Another goal is to evaluate putative paintbrush hybrids. We have determined that they can produce viable seeds, and the next step is to verify that they are indeed hybrids by determining whether they contain genes from both paintbrush species. Thus far, our results suggest a need to keep these species spatially separated.

Finally, workshop participants were asked to identify "no regrets" actions that could be implemented by managers to proceed with specific recovery actions in spite of uncertainties. Sometimes these actions could be identified by focusing on the overall ecosystem and on species interactions, rather than on just the rare species of interest. For example, enhancing the abundance and diversity of native prairie species via intensive seeding, plugging, and weed control has improved overall prairie quality even when direct benefits to either checkerspots or paintbrush may still be under debate, since we have limited information about "optimal" habitat for either organism. Similarly, planting multiple checkerspot host species, rather than just one, can act as an insurance policy to increase the likelihood that checkerspot populations are sustained by one or more host species. We have also agreed that planting checkerspot resources (both nectar plants and larval hosts) in multiple concentrated patches, rather than diffuse populations, is beneficial based on the tendency for checkerspots to aggregate, and has no obvious negative consequences for golden paintbrush. Finally, we have begun to release small quantities of captive-reared larvae onto golden paintbrush populations in deep-soil areas. While uncertainty remains about the suitability of golden paintbrush for this purpose, we concluded the potential benefits of establishing checkerspot populations here, in addition to the learning opportunities such releases afford, far outweigh the risks, especially since we are able to monitor the larvae and learn how they behave in this environment.

CONCLUSIONS

There are several ways in which recovery efforts for Taylor's checkerspot and golden paintbrush conflict, but there are also significant opportunities to cooperate, helping to achieve research and management objectives that advance recovery for both species. By convening workshops and implementing collaborative research, we have been able to clarify misunderstandings, build a common vision, and establish a shared research agenda. We have identified ways that recovery efforts can avoid hindering one another, and explored ways to use space, personnel, and funding more efficiently. By identifying no-regrets actions, we have been able to move ahead with recovery actions for rare species in spite of many uncertainties that have the potential to tie

the hands of both scientists and managers. By collaboratively seeking opportunities where benefits accrue to multiple rare species and to the ecosystem as a whole, and by carrying out such actions in ways that maximize learning, a balance between research and recovery can be found that fosters continued progress.

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LITERATURE CITED

Arnett, J. 2014. *Castilleja levisecta* global population estimates. Washington Natural Heritage Program, Washington Department of Natural Resources. Accessed 29 December 2014 <http://cascadiaprairieoak.org/documents/cale-global-pop-estimates-2014>.

Aubrey, D. 2013. Oviposition preference in Taylor's checkerspot butterflies (*Euphydryas editha taylori*): Collaborative research and conservation with incarcerated women. MS thesis, The Evergreen State College, Olympia, WA.

Barclay, E., M. Arnold, M. Andersen, and D. Shepherdson. 2009. Husbandry Manual: Taylor's Checkerspot (*Euphydryas editha taylori*). September 2009, 1st ed. Oregon Zoo, Portland, OR.

Bennett, V.J., M.G. Betts, and W.P. Smith. 2014. Influence of thermal conditions on habitat use by a rare spring-emerging butterfly *Euphydryas editha taylori*. Journal of Applied Entomology 138:623-634.

Bennett, V.J., S.M. Pack, W.P. Smith, and M.G. Betts. 2013. Sex-biased dispersal in a rare butterfly and the implications for its conservation. Journal of Insect Conservation 17:949-958.

Bennett, V.J., W.P. Smith, and M.G. Betts. 2012. Evidence for mate guarding behavior in the Taylor's checkerspot butterfly. Journal of Insect Behavior 25:183-196.

Boersma, P.D., P. Kareiva, W.F. Fagan, J.A. Clark, and J.M. Hoekstra. 2001. How Good Are Endangered Species Recovery Plans? BioScience 51:643-649. doi:10.1641/0006-3568(2001)051[0643:HGAESR]2.0.CO;2.

Bowers, M.D., N.E. Stamp, and S.K. Collinge. 1992. Early stage of host range expansion by a specialist herbivore, *Euphydryas phaeton*. Ecology 73:526-536.

Chadès, I., J.M.R. Curtis, and T.G. Martin. 2012. Setting realistic recovery targets for two interacting endangered species, sea otter and northern abalone. Conservation Biology 26:1016-1025.

Chappell, C., and F. Caplow. 2004. Site characteristics of golden paintbrush populations. Natural Heritage Report 2004–03, Washington Natural Heritage Program, Washington Department of Natural Resources, Olympia, WA.

Chiba, S. 2010. Invasive non-native species' provision of refugia for endangered native species. Conservation Biology 24:1141-1147. doi:10.1111/j.1523-1739.2010.01457.x.

Delvin, E.G. 2013. Restoring abandoned agricultural lands in Puget lowland prairies: A new approach. PhD Dissertation, University of Washington, Seattle.

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.

Dunwiddie, P.W., R. Davenport, and P. Speaks. 2001. Effects of burning on *Castilleja levisecta* at Rocky Prairie Natural Area Preserve, Washington: A summary of three long-term studies. Pp. 161–172 *in* S.H. Reichard, P.W. Dunwiddie, J. Gamon, A.R. Kruckeberg, and D.L. Salstrom, eds. Conservation of Washington's Native Plants and Ecosystems. Washington Native Plant Society, Seattle.

Dunwiddie, P.W., and R.A. Martin. 2016. Microsites matter: Improving the success of rare species reintroductions. PLoS One 11(3):e0150417. doi:10.1371/journal.pone.0150417.

Ehrlich, P.R., and I. Hanski, eds. 2004. On the Wings of Checkerspots. Oxford University Press, Oxford, U.K.

Falk, D.A., C.I. Millar, and M. Olwell. 1996. Part V. Guidelines for developing a rare plant reintroduction plan. Pp. 453–490 *in* D.A. Falk, C.I. Millar, and M. Olwell, eds., Restoring Diversity: Strategies for Reintroduction of Endangered Plants. Island Press, Washington, DC.

Federal Register. 1997. Endangered and Threatened Wildlife and Plants; Determination of Threatened status for *Castilleja levisecta*. Federal Register 62:31740-31748.

Gamon, J., P.W. Dunwiddie, T. Thomas, and T. Rush. 2001. Assessing the viability of golden paintbrush (*Castilleja levisecta*). Pages 51–58 *in* S.H. Reichard, P.W. Dunwiddie, J. Gamon, A.R. Kruckeberg, and D.L. Salstrom, eds. Conservation of Washington's

Native Plants and Ecosystems. Washington Native Plant Society, Seattle.

Godt, M.J.W., F. Caplow, and J.L. Hamrick. 2005. Allozyme diversity in the federally threatened golden paintbrush, *Castilleja levisecta* (Scrophulariaceae). Conservation Genetics 6:87-99.

Graves, S.D., and A.M. Shapiro. 2003. Exotics as host plants of the California butterfly fauna. Biological Conservation 110:413-433.

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

Gumm, J.M., J.L. Snekser, J.M. Leese, K.P. Little, J.K. Leiser, V.E. Imhoff, B. Westrick, and M. Itzkowitz. 2011. Management of interactions between endangered species using habitat restoration. Biological Conservation 144:2171-2176. doi:10.1016/j.biocon.2011.05.006.

Hanski, I., P.R. Ehrlich, M. Nieminen, D.D. Murphy, J.J. Hellmann, C.L. Boggs, and J.F. McLaughlin. 2004. Checkerspots and conservation biology. Pp. 264–287 *in* P.R. Ehrlich and I. Hanski, eds., On the Wings of Checkerspots, A Model System for Population Biology. Oxford University Press, Oxford, U.K.

Heckard, L.R. 1962. Root parasitism in *Castilleja*. Botanical Gazette 124:21-29.

Kaye, T.N., and M. Blakeley-Smith. 2008. An evaluation of the potential for hybridization between *Castilleja levisecta* and *C. hispida*. Washington Department of Natural Resources and the Institute for Applied Ecology, Corvallis, OR.

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.

Lee, S.D., P.G. Jabłoński, and H. Higuchi. 2007. Effect of heterospecifics on foraging of endangered red-crowned and white-naped cranes in the Korean Demilitarized Zone. Ecological Research 22:635-640. doi:10.1007/s11284-006-0067-z.

Linders, M., and K. Lewis. 2013. Captive rearing and translocation of Taylor's checkerspot butterfy (*Euphydryas editha taylori*): South Puget Sound, Washington, 2012–2013. 2013 Annual Report, Washington Department of Fish and Wildlife, Olympia.

Linders, M., K. Lewis, and L. Hamilton. 2014. Taylor's checkerspot (*Euphydryas editha taylori*) captive rearing and reintroduction: South Puget Sound, Washington, 2013–2014. 2014 Annual Report, Washington Department of Fish and Wildlife, Olympia.

Oro, D., A. Pérez-Rodríguez, A. Martínez-Vilalta, A. Bertolero, F. Vidal, and M. Genovart. 2009. Interference competition in a threatened seabird community: A paradox for a successful conservation. Biological Conservation 142:1830-1835. doi:10.1016/j.biocon.2009.03.023.

Pearson, S., and P. Dunwiddie. 2006. Experimental outplanting of golden paintbrush (*Castilleja levisecta*) at Glacial Heritage and Mima Mounds, Thurston County, WA. Washington Department of Natural Resources, Olympia.

Raphael, M.G., and R. Molina. 2007. Conservation of Rare or Little-Known Species: Biological, Social, and Economic Considerations. Island Press, Washington, DC.

Schultz, C.B. 2001. Restoring resources for an endangered butterfly. Journal of Applied Ecology 38:1007-1019.

Severns, P.M., and G.A. Breed. 2014. Behavioral consequences of exotic host plant adoption and the differing roles of male harassment and female movement in two checkerspot butterflies. Behavioral Ecology and Sociobiology 68:805-814.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era? Biological Conservation 83:247-257.

Singer, M.C., and C.S. McBride. 2009. Multitrait, host-associated divergence among sets of butterfly populations: Implications for reproductive isolation and ecological speciation. Evolution 64:921-33. doi:10.1111/j.1558-5646.2009.00866.x.

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.

Soulé, M.E., J.A. Estes, B. Miller, and D.L. Honnold. 2005. Strongly interacting species: Conservation policy, management, and ethics. BioScience 55:168-176.

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

Tear, T.H., J.M. Scott, P.H. Hayward, and B. Griffith. 1995. Recovery plans and the Endangered Species Act: Are criticisms supported by data? Conservation Biology 9:182-195.

[USFWS] US Fish and Wildlife Service. 2000. Recovery Plan for the Golden Paintbrush (*Castilleja levisecta*). US Fish and Wildlife Service, Portland, OR.

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.