Restoring resources for an endangered butterfly

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Summary

1. Recent changes in land use have resulted in dramatic habitat loss for numerous species. More than 99% of the habitat for Fender’s blue butterfly *Icaricia icarioides fenderi*, an endangered butterfly in Oregon, USA, has been lost.
2. Fender’s blue butterflies require larval host-plants (Kincaid’s lupine *Lupinus sulphureus kincaidii*) and nectar from native wildflowers.
3. An experiment was conducted at two degraded sites near Eugene, Oregon, to investigate methods for restoration of Fender’s blue habitat. The experimental design included four soil treatments (tilling, reverse fertilization, solarization and a control) combined with two planting treatments (50% forb seed : 50% grass seed and 10% forb seed : 90% grass seed) and two weeding treatments (weeding or not weeding). Treatments were replicated in eight experimental blocks (9 × 28 m) at each site. Seeds from 12 native plant species were field collected and sown in September 1995.
4. Plant establishment was monitored in May 1996, 1997, 1998 and 1999. In 1999, flowers of all nectar species and leaves of Kincaid’s lupine were counted.
5. Based on estimates of resource needs from previous work, resources were evaluated as insufficient, sufficient or ample.
6. Solarization combined with 50% forb : 50% grass planting promoted sufficient nectar to sustain butterflies at both sites. Control treatments provided insufficient nectar at both sites. None of the treatments produced sufficient larval resources.
7. This experiment demonstrates a method to quantitatively link habitat restoration to the resource needs of focal species. The results emphasize the importance of connecting restoration efforts to the life-history features of focal species. In addition, they highlight the importance of using experiments conducted across a range of sites to test restoration methods before large-scale efforts are implemented.

Key-words: Fender’s blue butterfly *Icaricia icarioides fenderi*, habitat restoration, Kincaid’s lupine *Lupinus sulphureus kincaidii*, larval host-plant, nectar.

Introduction

Habitat loss is the leading cause of species endangerment. Habitat restoration is quickly becoming part of the conservation plans for most endangered species (Schemske *et al*. 1994; Dobson, Bradshaw & Baker 1997; Wilcove & Chen 1998). Endangered insects often depend on habitat restoration because their natural habitats are frequently so scarce and isolated that maintaining existing habitat is not sufficient for insect species to recover their numbers (Schultz & Chang 1998; Assmann & Janssen 1999). Habitat restoration relies on understanding the essential features of endangered species’ habitats and the ecological processes necessary to achieve habitat renewal (Pavlik 1996).

Restoring habitat for endangered species involves at least four steps: characterizing the habitat of focal species, selecting restoration sites, conducting restoration activities, and evaluating results in the context of the focal species. Many restoration attempts have failed due to insufficient ecological knowledge or planning (Pullin 1996; Montalvo *et al*. 1997). For example, Pullin (1996) warns that one of the most common reasons why restoration of butterfly populations fails in Britain is the lack of knowledge of focal species’ requirements. Since the late 1980s, as few as 8% of 323 butterfly reintroduction attempts have succeeded (Pullin 1996).

Site selection, an important part of restoration planning, often involves evaluating the historical distribution of appropriate habitat as well as considering current land usage (Fiedler & Laven 1996; Pullin 1996;
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Another part of planning involves designing projects that allow the evaluation of results and generalization to other similar situations. Currently, many restoration activities utilize a single technique for a unique site. This makes it difficult to generalize about the success or failure of the techniques applied (Michener 1997). For example, the reasons for restoration are diverse (i.e. presence of non-indigenous species vs. highly polluted soils) and techniques tested at one site for one set of problems may not generalize to other situations, even in attempts to restore the same habitat type. Experiments that investigate processes to recreate habitats are useful in designing restoration projects because they provide a mechanism to generalize techniques to a range of situations (Carlsen, Menke & Pavlik 2000).

Finally, project evaluation should provide quantitative estimates of essential habitat features for focal species. Insufficient or improper monitoring has plagued many restoration efforts, which makes it difficult to evaluate their success (Pavlik 1996). For example, Fiedler (1991) found that only 15 of 46 plant re-introduction attempts defined explicit criteria for success.

This study investigated habitat restoration for Fender’s blue butterfly *Icaricia icarioides fenderi* (Macy), an endangered butterfly in Oregon, USA (Anonymous 2000). This butterfly provides an ideal model system in which to investigate habitat restoration for endangered species for several reasons. First, its habitat requirements are relatively easy to define. Habitat includes three key features: larval host-plant (*Kincaid’s lupine, Lupinus sulphureus kincaidii*), native forbs for nectar sources, and grasses and forbs that help maintain the historical short-grass structure of the upland prairies (Wilson, Hammond & Schultz 1997). In addition, previous research provides quantitative estimates of the butterfly’s resource needs. Schultz & Dlugosch (1999) suggest that suitable habitat for adult Fender’s blue butterflies supports approximately 20 mg sugar m⁻² of nectar from native flower species, and that suitable habitat for larval butterflies supports approximately 40 leaves m⁻² of appropriate larval host-plant.

Second, appropriate sites for restoration are easily identifiable. For this study, initially sites were considered that were likely to have historically supported Willamette Valley upland prairies, the habitat type upon which Fender’s blue butterflies persist. Of five sites that met requirements for upland prairie, two sites were selected for a major restoration experiment. Site selection relied on site-based features, such as site history, and landscape-level features, such as distance from nearby Fender’s blue populations. Previous research on Fender’s blue suggests that, to promote movement throughout the region, the butterfly requires stepping stones of habitat separated by less than 1 km (Schultz 1998). Chosen sites, once restored, have the potential to serve as stepping stones and promote butterfly movement between prairie remnants in the Willamette Valley. Weedy agricultural fields are the most common type of vegetation in areas that were historically Fender’s blue butterfly habitat. Therefore, an experiment was designed to test methods to establish important plant species in old agricultural fields.

Third, although there have been no prior attempts to restore upland prairie in Willamette Valley, much is known about restoring upland prairies in the mid-western US, as well as restoration of wetland prairies in the Willamette Valley (Howell & Jordan 1991; Wilson et al. 1995; Packard & Mutel 1997). The current research experimentally investigated how to restore upland prairie habitat across a range of conditions. Finally, evaluation of treatments is directly tied to butterfly resource needs because resource usage is well understood.

This paper provides details of 5 years of a study that investigated habitat restoration for Fender’s blue butterfly. Two primary factors were investigated that influence the ability of desired native plants to outcompete non-indigenous weeds: soil preparation before sowing, and the relative forb to grass composition at sowing. It was predicted that (i) variation in soil preparation would modify the strength of weed competition by removing existing weeds and reducing the density of weed seeds in the soil, and (ii) changing the physical structure of the plant community by increasing the forb : grass ratio would increase establishment rates by sown forbs because the low-stature forbs would have higher survivorship when surrounded by fewer tall grasses. In 1995, sites were prepared for the experiment and seeds collected and planted. In the ensuing 4 years, plant establishment was monitored. In 1999, the success of the plantings was assessed as potential butterfly resources.

### Materials and methods

#### Site description

Willamette Valley grasslands in the north-western United States were historically a mosaic of upland and wetland prairie (Alverson 1993). Less than 0.5% of the original upland prairies remain (Alverson 1993). Three of the 12 remnants of upland prairie that support Fender’s blue butterflies are near Eugene, Oregon. One of these areas, The Nature Conservancy’s Willow Creek Natural Area, supports one of the two largest remaining Fender’s blue populations. About 5 ha of upland habitat at Willow Creek supports a population of 500–1500 Fender’s blue butterflies (Schultz & Fitzpatrick 1999).

Recent land acquisitions by the US Bureau of Land Management (BLM) and The Nature Conservancy include several upland areas that have potential to be restored as Fender’s blue habitat. Two areas in
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particular are well suited for experiments investigating methods to restore the butterfly’s habitat: a 12-ha field at Willow Creek (44°N, 123°W) and a 5-ha BLM property, Royal (44°N, 123°W). These fields contain a diverse set of weedy, herbaceous species, few of which are native to the area. The species composition of the weed community differs greatly between the sites (Schultz 1997). Royal has a high weed diversity and a relatively high plant biomass. In contrast, Willow Creek has relatively low weed diversity, shorter and sparser grasses, and a much lower biomass. The differences between these fields make them an ideal pair of sites to investigate techniques for upland prairie restoration. Because the two fields differ, if the same technique successfully restores butterfly habitat in both places, then the technique may be widely applicable in other restorations. If the technique gives different results in each field, then we know we must fine-tune future restoration efforts. In addition, because the location of these field makes them well-suited to serve as stepping stones for butterfly dispersal between existing populations, if the technique works at a small experimental scale, then the approach can be applied at a larger scale in that field.

EXPERIMENTAL DESIGN

The experimental design was a split-plot within randomized complete block design (Fig. 1). Blocks were 9 × 28 m, large enough for large farm vehicles such as tractors to implement the treatments. Each block had five soil preparations: two tilling treatments, a solarization treatment, a reverse fertilization treatment, and a control. Tilling is a common restoration tactic because it removes most of the existing vegetation and creates open space for newly planted species (Howell & Jordan 1991). In this analysis, the two tilling treatments within each block were identical. Solarization involves laying sheets of clear plastic over freshly tilled soil. The edges are buried about 20 cm deep, which creates a seal that traps heat during the summer months. Thus, solarization further reduces the effects of competition from weeds (Cooley 1985; Egley 1990; Hartz, DeVay & Elmore 1993). Reverse fertilization is a method that sometimes facilitates the establishment of native plant species by restoring historically nutrient-poor soil conditions (Morgan 1994; K. Davis & M. V. Wilson, unpublished data). The technique reduces available soil nitrogen by adding carbon to the soil, a process that allows soil bacteria to consume the carbon amendment, thus rendering nitrogen unavailable to growing plants (Lamb 1980; Hunt et al. 1988; McClendon & Redente 1992). The positions of soil treatments within each block were randomized, and blocks were replicated eight times at Willow Creek and eight times at Royal.

The historical plant composition of Willamette Valley upland prairies is unknown (Franklin & Dyrness 1987). Currently, even relatively intact prairies are dominated by invasive plants (Wilson et al. 1995). In restoration projects in the tallgrass prairies of the midwestern U.S., forb to grass ratios, in terms of numbers of seeds, have ranged from 40:60 to 10:90 (Howell & Jordan 1991). Forb to grass densities were manipulated at two levels. The treatment with a high forb:grass density contained approximately 50% forb seed and 50% grass seed, and the low forb:grass density contained approximately 10% forb seed and 90% grass seed. Within each soil treatment preparation, two 2·25-m² plots were placed randomly for experimental sowing.

Native plants sown in the experiment included a dozen native species found near the study sites: Kincaid’s lupine, four forb species used as nectar sources by butterflies.
Fender’s blue butterflies (*Allium amplectans*, *Camassia quamash*, *Eriophyllum lanatum* and *Sidalcea virgata*), three additional forbs (*Fragaria virginiana*, *Lupinus bicolor* and *Potentilla gracilis*) and four grasses (*Danthonia californica*, *Elymus glaucus*, *Festuca roemeri* and *Festuca rubra var. commutata*) (plant nomenclature follows Hitchcock & Cronquist 1973). All seeds were collected within 10 km of the study sites. In addition, bulbs were salvaged from *Camassia* from an area that was in the early stages of urban development. Planting densities relied on amount of available seed, with a maximum for grass seed set at 1 seed cm$^{-2}$ based on analyses of the density of seeds in the seed bank (Wilson, Ingersoll & Wilson 1994).

The nectar sources in this experiment were chosen for several specific reasons. First, these species provided a better source of sugar than other, particularly non-native, nectar sources (Schultz & Dlugosch 1999). Second, these plants represented a phenological range, flowering from late April until mid-June. Third, the nectar species were chosen because they were abundant enough to provide adequate seed for the experiment. More than 100 000 *Eriophyllum* seeds and 45 000 *Sidalcea* seeds were planted, which required significant sources for seed (Table 1). Species such as *Geranium oreganum* and *Iris tenax* provide excellent nectar (Schultz & Dlugosch 1999), but were not abundant enough for the purposes of this experiment.

Special consideration was given to establishment of Kincaid’s lupine because it is a key resource for Fender’s blue butterfly and is a federally listed threatened species (Anonymous 2000). Much about the basic biology of Kincaid’s lupine is unknown (Kuykendall & Kaye 1993). This research is among the first attempts to re-introduce Kincaid’s lupine experimentally. To maintain the genetic integrity of local populations, all seeds were collected from the population closest to each restoration site. Seeds planted at Willow Creek were collected from lupine populations on other parts of the preserve. Similarly all seeds planted at Royal were collected from Fir Butte, a lupine population a few kilometres from Royal. All seeds were scarified with a file, and planted individually in the field. A handful of soil from the seed source was planted with each seed to provide a source of native mycorrhizae. This method was pilot-tested in 1993 (Schultz 1994). Unfortunately, even though over 10 000 seeds were planted in autumn 1995, few were observed the following spring (Table 2). Therefore, two methods of planting were tested the following year. First, in the event that 1995 was a bad year for lupine establishment, the same seeding method was used for 1280 seeds site$^{-1}$. Second, seeds were germinated in the University of Washington greenhouse in March 1997 and transplanted to the field a few weeks later, at which point each plant had two cotyledons plus one to three true leaves. Due to the limited supply of seeds that year, there were only 160 plants to transplant to the field. The lupines were planted at a rate of one plant per 2.25-m$^2$ plot. Because the transplant

### Table 1. Plants sown as nectar sources

<table>
<thead>
<tr>
<th>Plant stage</th>
<th>Site</th>
<th>Total number planted</th>
<th>Plants in 1996</th>
<th>Plants in 1997</th>
<th>Plants in 1998</th>
<th>Plants in 1999</th>
</tr>
</thead>
<tbody>
<tr>
<td>High forb plots</td>
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<tr>
<td>Low forb plots</td>
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<table>
<thead>
<tr>
<th>Species</th>
<th>Site</th>
<th>Plants (plants plot$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Allium amplectans</em></td>
<td>Willow Creek</td>
<td>135</td>
</tr>
<tr>
<td><em>Camassia quamash</em></td>
<td>Royal</td>
<td>155</td>
</tr>
<tr>
<td><em>Eriophyllum lanatum</em></td>
<td>Willow Creek</td>
<td>8</td>
</tr>
<tr>
<td><em>Sidalcea virgata</em></td>
<td>Royal</td>
<td>900</td>
</tr>
</tbody>
</table>

*Allium amplectans* was not counted. See text for details. **Camassia quamash** were eaten by deer before the 1996 census at Royal.
A technique appeared more successful, it was repeated on a larger scale the following year (April 1998).

Budelsky & Galatowitsch (2000) have recently confirmed that competition from weeds in the early stages of plant establishment may critically influence long-term restoration success. To investigate the influence of limited post-planting efforts to reduce competition from weeds, each 2.25-m² sown plot was divided in half. A randomly chosen half received a weeding treatment and the second half received no ongoing management. In each weeded area, non-native forbs were clipped at the base to minimize disturbance to nearby focal species. Non-native grasses was not removed because it was difficult to distinguish native from non-native species early in the season, the time of weeding. Weeds were removed for up to 30 min in each plot because half an hour of labour per square metre of restored area was near the upper limit in labour that would probably be available to restore habitat at a larger scale.

**Experiment Implementation**

Soil treatments were initiated in spring and summer 1995. In May, all areas were mowed. This was followed by establishing experimental plots and tilling all areas except the controls in June and early July. Solarization was begun in early July. Solarization traps moisture that conducts heat and causes some seeds to germinate, seedlings that are then killed by the high temperatures (Egley 1990; Elmore, Roncoroni & Giraud 1993). Egley (1990) found that seedlings were killed in dry soil at around 70 °C, but in moist soil at temperatures as low as 50 °C. Because the soil was fairly dry by July, all areas were watered with assistance from the Eugene District BLM. Using fire trucks to provide water, the BLM sprayed approximately 10 000 gallons of water over each site. The plastic was left on the soil from 8 July 1995 to 18 September 1995, at which time it was removed so that seeds could be planted.

Seeds were collected during June and July 1995 and cleaned at Oregon State University in August. Seeds of *Sidalcea* and *Lupinus bicolor* were scarified in groups of a few hundred with a small sanding tool. In mid-September, seeds were planted in the experimental areas. Based on consultation with a local soil biologist (E. Ingham, Oregon State University, personal communication), sugar was chosen as the carbon amendment in this study. Sugar was spread over the reverse fertilization plots in early February 1996, at the beginning of the spring growing season. The amount of sugar added to each plot was calculated based on the methods of Hunt *et al.* (1988), which was calibrated to immobilize the soil nitrogen in the top 10 cm of soil. This resulted in additions of 650 g sugar m⁻² at Royal, and 500 g sugar m⁻² at Willow Creek. The weeding treatment was applied in April 1996 and 1997. To reduce deer herbivory, fences were built around the experimental areas in November 1995 (Willow Creek) and late April 1996 (Royal).
ASSESSMENT OF EXPERIMENT

To evaluate the direct effect of the soil treatment on weeds, in April 1996 all plants were removed from four randomly placed 15 × 50-cm quadrats outside the sown plots but within each soil treatment area. The plants were dried clipped to a constant weight for measurement of weed biomass. To determine the effects of the reverse fertilization treatment, soil nitrogen was assessed. In June 1996, soil nitrogen was measured by taking five random samples in each reverse fertilization plot and an equal number in each tilled plot. The Central Analytical Laboratory at Oregon State University analysed the samples. To assess the effects of the solarization treatments, soil thermometers were placed under the sealed plastic. Soil temperatures in solarized and unsolarized plots were measured weekly at soil depths of 4 cm and 8 cm.

ASSESSMENT OF RESOURCE ESTABLISHMENT

To evaluate nectar and host-plant establishment, all focal species [Camassia (from bulb only), Eriophyllum, L. sulphureus and Sidalcea] were counted once each spring of 1996, 1997, 1998 and 1999. Allium and Camassia seedlings were not monitored because they were extremely difficult to identify as non-reproductive plants.

Resource abundance was evaluated in 1999, when many of the nectar plants had begun to flower, by counting the number of flowers of each focal species. Total available nectar sugar was estimated by multiplying the number of flowers by the amount of nectar per flower, based on estimates of sugar per flower in Schultz & Dlugosch (1999). Based on correlating nectar abundance with butterfly density across several sites, a Fender’s blue butterfly population requires flower density equivalent to 20 mg sugar m⁻² to provide sufficient nectar (Schultz & Dlugosch 1999). Nectar production in the experiment was judged to be ‘insufficient’ if nectar levels were significantly less than 20 mg sugar m⁻², ‘sufficient’ if nectar levels were no different than 20 mg sugar m⁻² and ‘ample’ if the nectar levels were significantly more than 20 mg sugar m⁻². To assess abundance of Kincaid’s lupine (the larval resource), leaves on all Kincaid’s lupine plants were counted and leaf density compared with that suggested by Schultz & Dlugosch (1999) (40 leaves m⁻²) as the minimum leaf density required to support larvae to pupation.

STATISTICAL ANALYSIS

To evaluate treatment effects on nectar plant establishment, repeated-measures ANOVA in SYSTAT (Wilkinson, Hill & Vang 1992) was used. Count data were log-transformed to improve normality in the data (Sokal & Rohlf 1981). After initial effects were identified in the full model, pairwise interactions were looked at for all significant effects, as suggested by Barker & Barker (1984). Because lupines established in only a few plots, treatments were first analysed using stepwise logistic regression to assess whether or not treatments affected plant establishment. Then repeated-measures ANOVA was used to determine if the treatments affected the level of establishment. The same approach was used to assess the effects of the treatments on the abundance of nectar flowers and the overall level of available sugar in 1999. To test whether resource production was ‘sufficient’, one-sample t-tests were used to test if the nectar levels differed from 20 mg sugar m⁻² or if Kincaid’s lupine leaf densities differed from 40 leaves m⁻².

RESULTS

DIRECT EFFECTS OF SOIL TREATMENTS

There were significantly more weeds at Royal than Willow Creek in each soil treatment (two-way ANOVA, site factor F[3,51] = 41.6, P < 0.0001, treatment factor F[3,51] = 12.5, P < 0.0001, pairwise comparisons of weeds between sites for each treatment using Bonferroni procedure to adjust for multiple comparisons, P < 0.05 for controls, P < 0.001 for other treatments; Fig. 2). At both sites, there were significantly more weeds in the control plots than the manipulative treatments (tiling, solarization and reverse fertilization, P < 0.05, pairwise comparisons from two-way ANOVA above). The manipulative soil treatments produced different effects at the two sites. At Willow Creek, weeds were significantly less abundant in the solarization plots than the tilling plots (F = 0.06, pairwise comparison from two-way ANOVA above). The effect of reverse fertilization was intermediate between the tilling and the solarization (F > 0.10 for both comparisons, pairwise comparisons from two-way ANOVA above). At Royal, all manipulative treatments were significantly better at reducing weeds than the control, but no manipulative effect was different from any other (F > 0.3 for all comparisons between manipulative treatments, pairwise comparisons from two-way ANOVA above).

![Fig. 2. Direct effect of soil treatments on the weed community. Weeds were clipped from inside treatment areas but outside sown plots. Filled bars, Royal; open bars, Willow Creek. See text for details.](image-url)
Reverse fertilization did not cause changes in soil nitrogen. Although the sites were significantly different (mean soil nitrogen was 7.1 ± 4.5 p.p.m. at Royal and 3.5 ± 0.7 p.p.m. at Willow Creek, two-way ANOVA, F_{1,28} = 9.96, P = 0.004), there were no significant differences in total nitrogen content between reverse fertilization plots and tilled plots at either site (two-way ANOVA, F_{1,28} = 0.96, P = 0.34, pairwise comparisons from June 1996 soil analysis, P = 0.52 at Royal and P = 0.15 at Willow Creek). Solarization increased soil temperatures. Soil under the plastic was 7.5–2.4 °C warmer at 4 cm and 8.0–2.9 °C warmer at 8 cm than non-solarized plots (at Royal: t_{11} = 6.3, P < 0.001 at 4 cm, t_{11} = 6.2, P < 0.001 at 8 cm; at Willow Creek: t_{12} = 3.0, P < 0.012 at 4 cm, t_{12} = 4.7, P < 0.001 at 8 cm). The peak solarization temperature was 32 °C.

**ESTABLISHMENT OF NECTAR PLANTS, THE ADULT RESOURCE**

Three species of nectar plants established and flowered: *Camassia*, *Eriophyllum* and *Sidalcea* (Table 1). Although a few non-reproductive *Allium* plants were observed in 1996 and 1997, none was observed to flower by 1999. Transplanted bulbs, not seeds, were responsible for all observed *Camassia* flowers. Repeated-measures ANOVA indicated that site, soil treatment and seeding ratio had significant effects on nectar plant establishment (Fig. 3 and Table 3). In addition, site by treatment and site by planting interactions were also important.

Approximately one of every four *Camassia* bulbs successfully re-established (Table 1). Many *Camassia* plants were not counted in 1996 because of herbivory at Royal before the fence was built. By 1999, the number of *Camassia* was increasing, probably due to reproductive splitting of bulbs (Fig. 3a,b). Soil treatments had small effects on *Camassia* establishment at Royal, but very noticeable initial effects at Willow Creek. In 1996 and 1997, there were fewer plants in the controls than in the manipulative soil treatments, but by 1998 and 1999 the differences were less dramatic (Fig. 3). *Eriophyllum* established in larger numbers at Willow Creek than Royal (Fig. 3c,d). Pairwise comparisons between soil treatments at each site indicated that there were no significant differences between treatments at Royal. However, at Willow Creek solarization and tilling were better at supporting *Eriophyllum* than both

![Fig. 3. Effect of soil treatments on nectar plant establishment and survivorship. Filled circles, tilling treatment; open circles, solarization treatment; filled triangles, reverse fertilization treatment; open triangles, control treatment. (a) *Camassia* at Willow Creek; (b) *Camassia* at Royal; (c) *Eriophyllum* at Willow Creek; (d) *Eriophyllum* at Royal; (e) *Sidalcea* at Willow Creek; (f) *Sidalcea* at Royal.](image-url)
control and reverse fertilization treatments \((P < 0.001)\) for pairwise comparisons from ANOVA in Table 3. Bonferroni method used to adjust for multiple comparisons. In addition, more Eriophyllum plants established in high forb plantings than low forb plantings at Willow Creek \((P < 0.001,\) pairwise comparison from ANOVA in Table 3), but there were no differences between planting treatments at Royal.

In contrast, Sidalcea established in relatively large numbers at Royal but did not establish well at Willow Creek (Fig. 3c.f). There were no differences between soil treatments for Sidalcea at Willow Creek. At Royal, reverse fertilization and tilling supported more Sidalcea than the control or solarization treatments \((P < 0.001\) and \(P = 0.027\) for the reverse fertilization comparisons from ANOVA in Table 3; \(P < 0.001\) for both tilling comparisons from ANOVA in Table 3). At Royal, sowing a higher density of forb seeds resulted in more Sidalcea plants \((P < 0.001,\) pairwise comparison from ANOVA in Table 3), but at Willow Creek it did not have a significant impact.

Although many nectar plants established, only a fraction of them flowered by 1999 (Table 4). For all three species, site was the only significant factor influencing whether or not the plants flowered (Camassia: \(\chi^2 = 6.2, P = 0.013;\) Eriophyllum: \(\chi^2 = 24.9, P < 0.001;\) Sidalcea: no test because there were no flowers at Willow Creek; Table 5). The amount of nectar per plot ranged from 0 mg sugar m\(^{-2}\) to over 150 mg sugar m\(^{-2}\) (Table 5). Stepwise logistic regression indicated that site, planting and soil treatments were all significant factors affecting target seedling establishment (site: \(\chi^2 = 11.8, P = 0.001;\) planting: \(\chi^2 = 9.5, P = 0.002;\) tilling: \(\chi^2 = 10.5, P = 0.001;\) solarization: \(\chi^2 = 7.9, P = 0.005\)).

For those plots that produced nectar, ANOVA indicated that site and treatment significantly influenced the amount of sugar produced (Fig. 4; site factor \(F_{2,39} = 16.23, P < 0.0001,\) treatment factor \(F_{4,39} = 4.87, P = 0.004\)). The control treatment produced insufficient nectar relative to levels suggested by Schultz & Dlugosch (1999) for both high and low forb density plantings at both sites (Table 6 and Fig. 4). At Royal, all other

### Table 3: Summary of repeated-measures ANOVA for nectar species

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Camassia quamash</th>
<th>Eriophyllum lanatum</th>
<th>Sidalcea virgata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site (S)</td>
<td>MS 15.3</td>
<td>MS 28.4</td>
<td>MS 3.1</td>
</tr>
<tr>
<td>Treatment (T)</td>
<td>4.8</td>
<td>4.1</td>
<td>3.6</td>
</tr>
<tr>
<td>Planting (P)</td>
<td>9.8</td>
<td>0.0</td>
<td>9.1</td>
</tr>
<tr>
<td>Weeding (W)</td>
<td>14.9</td>
<td>9.8</td>
<td>14.9</td>
</tr>
<tr>
<td>X T</td>
<td>MS 244.8</td>
<td>MS 27.4</td>
<td>MS 18.5</td>
</tr>
<tr>
<td>Within subjects (temporal effects)</td>
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<td></td>
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<tr>
<td>Year (Y)</td>
<td>4.0</td>
<td>4.0</td>
<td>0.0</td>
</tr>
<tr>
<td>T 9</td>
<td>7.4</td>
<td>3.6</td>
<td>1.8</td>
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<tr>
<td>S X T</td>
<td>9.0</td>
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<tr>
<td>S X P</td>
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<td>S X T X P</td>
<td>2.7</td>
<td>0.0</td>
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</tr>
</tbody>
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*Other interactions were not significant except the following: between-subject effect for Camassia quamash for S X P X W \((F_{3,29} = 2.7, P = 0.021)\) and for Eriophyllum lanatum for T X P \((F_{3,19} = 3.9, P = 0.01)\), and within subject for Eriophyllum lanatum for Y X S X T X P \((F_{4,19} = 2.5, P = 0.06)\).
treatments produced sufficient or ample levels of sugar.

At Willow Creek, all other high forb plantings resulted in sufficient sugar production, but only the solarization soil treatment produced enough sugar when a low forb seeding was applied.

### Table 5. Nectar species and sugar production for each planting by soil treatment combination at each site. Values for sugar content from Schultz & Dlugosch (1999). *Camassia quamash* contains 0.75 mg sugar per flower, *Eriophyllum lanatum* contains 3.86 mg sugar per flower and *Sidalcea virgata* contains 1.62 mg sugar per flower.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Planting</th>
<th>Royal</th>
<th>Willow Creek</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Flowers m$^{-2}$</td>
<td>SD</td>
<td>Flowers m$^{-2}$</td>
</tr>
<tr>
<td>Control</td>
<td>Forb</td>
<td>1.6</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>Grass</td>
<td>3.7</td>
<td>0.4</td>
</tr>
<tr>
<td>Reverse fertilization</td>
<td>Forb</td>
<td>2.6</td>
<td>0.0</td>
</tr>
<tr>
<td>Solarization</td>
<td>Forb</td>
<td>6.5</td>
<td>10.3</td>
</tr>
<tr>
<td></td>
<td>Grass</td>
<td>5.7</td>
<td>12.9</td>
</tr>
<tr>
<td>Till</td>
<td>Forb</td>
<td>6.0</td>
<td>19.8</td>
</tr>
<tr>
<td></td>
<td>Grass</td>
<td>4.6</td>
<td>14.3</td>
</tr>
</tbody>
</table>

### Table 6. Treatments with sufficient levels of nectar. Responses of 1-sample t-tests testing if nectar per treatment is less than 20 mg sugar m$^{-2}$ (insufficient sugar), not significantly different than 20 mg sugar m$^{-2}$ (sufficient sugar) or more than 20 mg sugar m$^{-2}$ (ample sugar). Results are scored as I, S or A, respectively.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Planting</th>
<th>Royal</th>
<th>Willow Creek</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Flowers m$^{-2}$</td>
<td>SD</td>
<td>Flowers m$^{-2}$</td>
</tr>
<tr>
<td>Control</td>
<td>Forb</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>Grass</td>
<td>1.7</td>
<td>5.1</td>
</tr>
<tr>
<td>Reverse fertilization</td>
<td>Forb</td>
<td>63.8</td>
<td>83.4</td>
</tr>
<tr>
<td>Solarization</td>
<td>Forb</td>
<td>40.7</td>
<td>67.6</td>
</tr>
<tr>
<td></td>
<td>Grass</td>
<td>16.7</td>
<td>42.8</td>
</tr>
<tr>
<td>Till</td>
<td>Forb</td>
<td>90.0</td>
<td>117.5</td>
</tr>
<tr>
<td>Solarization</td>
<td>Grass</td>
<td>30.3</td>
<td>63.3</td>
</tr>
</tbody>
</table>

At Willow Creek, all other high forb plantings resulted in sufficient sugar production, but only the solarization soil treatment produced enough sugar when a low forb seeding was applied.

### ESTABLISHMENT OF KINCAID’S LUPINE, THE LARVAL RESOURCE

Although over 12,000 seeds were sown and 600 seedlings transplanted, there were fewer than 60 plants by 1999 (Table 2). Less than 10% of seeds planted in 1996 germinated and survived long enough to be counted in the May 1997 census. Initial observations of transplanted seedlings died by the following May (Table 2). Once plants reached one year of age, they had a much higher rate of survival: almost 70% of yearlings survived until their second year and about 40% of second-year plants were observed as 3-year-olds.

Because so few lupines survived, the abundance of this resource was very limited in 1999. A total of 74 Kincaid’s lupine leaves was counted at Royal and 315 leaves at Willow Creek. The leaves were not equally distributed. At Royal, 43 leaves were on three of 12 plants at the site in 1999; at Willow Creek 75 of the leaves were on a single plant.
Discussion

This set of experiments succeeded in restoring some aspects of Fender’s blue butterfly habitat. Plants providing nectar resources for adult butterflies became established in several treatments at both sites (Fig. 4). Larval resources, however, were not present in sufficient numbers to support a butterfly population 4 years after planting (Table 2). Soil preparation modified the strength of weed competition (Fig. 2). Alteration in the physical structure of the plant community, via changes in the relative forb and grass components in the community, influenced the establishment rates of sown forbs (Table 5). This study provides some useful general insights regarding restoration of habitat for endangered species. Because food plants for a wide range of bird and butterfly species are declining (Smart et al. 2000), methods to restore adequate resources will be essential in conservation planning for many species.

Results of the experimental treatments suggest that nectar resources are most likely to establish when soil solarization before planting is combined with a high sowing density of forbs. At both sites, solarization was most successful in reducing competition from weeds (Fig. 2). Solarization was the only treatment that provided sufficient nectar production at both sites (Fig. 4 and Table 6). Solarization increased soil temperature, which probably caused mortality of weed seeds and seedlings and of plant pathogens (Elmore, Roncoroni & Giraud 1993; Lopez-Herrera et al. 1999). It is worth noting that although solarization was conducted on a small scale in this study, it is based on a common technique in commercial agriculture. In southern California, strawberry growers cover many hectares of soil with plastic to prepare the soil for planting (Hartz, DeVay & Elmore 1993; C.B. Schultz, personal observation).

In this study, the effect of solarization was most pronounced at Willow Creek (Fig. 2). In contrast, the control treatment (sowing seeds into untilled soil) did not lead to establishment of nectar resources. However, sowing seeds into tilled soil might be sufficient to establish key resources at some sites. For example, at Royal there were no statistically significant differences in nectar production between tilling, reverse fertilization and solarization. Although reverse fertilization did not change nectar production here, this method deserves further investigation because reducing soil fertility is often a desired outcome in restoration (Mitchell et al. 1999) and because different amounts or frequencies of carbon amendment might influence the treatment outcome. For example, K. Davis & M. V. Wilson (personal communication) added sugar and sawdust to wetland prairies in the Willamette Valley in autumn and spring. They observed fewer weeds and higher establishment rates of native grasses after experimental carbon additions. Similarly, Reever-Morgan & Seastedt (1999) found that applying a combination of sugar and sawdust monthly to a Colorado perennial grassland reduced a problem weed, diffuse knapweed Centaurea diffusa. Callaway & Aschehoug (2000) experimentally demonstrated that allelopathic properties of diffuse knapweed inhibit native plant growth, an effect that further reinforces the need to reduce weeds before seeding native plants.

Many other methods have been investigated to restore grassland habitats. For example, in a mixed-grass prairie in Saskatchewan, Canada, Wilson & Gerry (1995) tilled soil and added herbicide and nitrogen to prepared plots to reduce weed cover. Their highest success in weed reduction resulted from simultaneous application of all three treatments. They hypothesize that such application creates ‘neighbour-free’ space for native plants to establish. In this study, the effects of weeding on nectar plants were negligible (Table 5). The labour invested in weeding was not sufficient to influence plant establishment. Although higher levels of weeding may have resulted in a positive response, the labour in this study was not increased because methods throughout the experiment were maintained at a level achievable in a large-scale restoration project.

In another study of grassland restoration, Hatch et al. (2000) investigated a variety of methods to restore California perennial grassland. They observed that one focal grass species, Doniumia californica, responded well to grazing treatments but not to fire treatments. In contrast, other focal grass species, Nasella lepida and N. pulchra, had varying responses to treatments. They caution that restoration treatments focusing on a single dominant plant species may be insufficient to restore a plant community.

Although many authors recognize the potential importance of initial seeding densities on the outcome of restoration efforts (Howell & Jordan 1991), few have experimentally manipulated these densities. One exception is the research by Carlisle, Menke & Pavlik (2000) investigating methods to restore perennial grassland habitat for Fender’s blue butterfly (Euchlaena manilaensis). They observed that a high density of native perennial or non-native annual grass inhibits Amsinckia flowe-

ring. However, at low and intermediate grass densities, Amsinckia has much higher flowering rates in native grass habitat than in non-native grass habitat. These results are consistent with present observations of restoration of Fender’s blue butterfly habitat in two ways. First, both studies suggest that sowing a lower grass density can enhance establishment of focal forb species. Second, when attempting to restore habitat for a rare species, an experimental approach is extremely useful in determining a prudent course of action in terms of relative planting densities of grasses and forbs.

Site differences caused very different responses to experimental treatments. At Willow Creek, solarization was the only treatment that promoted sufficient nectar production. At Royal, all treatments that began with tilling were similar in terms of nectar production (Fig. 4). Similarly, solarization significantly reduced...
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Restoring butterfly resources

weed growth at Willow Creek, but the trends were not as strong at Royal. These differences may, in part, result from lower soil nitrogen, weed biomass and weed diversity at Willow Creek. If these restoration techniques are applied to another potential site for Fender’s blue butterfly habitat, applying solarization techniques has the highest likelihood of providing adequate nectar production for the butterfly.

In contrast to the success in restoring nectar resources, Kincaid’s lupine experienced much lower success. The results from this study suggest that transplanting young seedlings may be more fruitful than sowing Kincaid’s lupine as seeds. Fortunately, there are several ongoing studies, and results from other efforts to establish Kincaid’s lupine are much more promising than those from this experiment. In a pilot planting in the autumn of 1993, 128 seeds were planted (Schultz 1994). Of these, eight plants established in 1994 and four were still alive in 1999. P. Severns (personal communication) planted 900 seeds adjacent to an existing lupine population in autumn 1997. Of these, 144 were established and survived to spring 2000. A. Kaye (personal communication) seeded lupine in an upland area adjacent to an experimental wetland restoration in autumn 1999. Twenty-four percent of these seeds survived to spring 2000. Variation between restoration sites includes plant diversity, plant biomass, land-use history and soil nutrients. Taken together, the preliminary results of this work suggest that seed source, sowing methods and restoration site may all significantly influence restoration of this endangered plant.

Herbivory is another ecological process that may influence the success of habitat restoration for the Fender’s blue butterfly. Native herbivores that may influence plant establishment include mammalian herbivores such as deer and voles and many species of insect herbivores. In this experiment, deer herbivory was reduced by constructing fences around the experimental areas. This was largely done because the experimental planting created small areas (2.25 m²) with young plants in a matrix of recently tilled, open soil. These areas were easy targets for deer to graze, as observed by the author when a deer grazed the blooming *Camassia* in each plot at Royal in early spring 1996. When restoration is scaled to the level of whole fields, it is expected that the relative effects of deer herbivores will be lower. The long-term influence of herbivores on restoration success is unknown and is a factor that should be considered in future experimental investigations.

Implications of This Research

The observed disparate responses of nectar species among sites in this study emphasizes that results from restoration efforts conducted at a single site are unlikely to be generalizable across a region. Similarly, in their study of salt marsh restoration at several sites in northern Canada, Handa & Jeffries (2000) concluded that the probability of native graminoid establishment was highly site specific. In this study, no single nectar species was highly successful at both sites. These results are consistent with suggestions about the importance of redundancy in ecological systems. Several authors have suggested that one significant function of biodiversity is that it enhances the reliability of a system (McGrady-Steed, Harris & Morin 1997; Naeem & Li 1997). In the case of restoring Fender’s blue butterfly habitat, planting several nectar species provides a much greater opportunity for sufficient nectar resources to establish.

Evaluation of these experimental treatments differs from evaluation of many restoration efforts. The most common method of evaluating restoration efforts is to compare features of a restored site to features of a ‘reference site.’ Reference sites are used to define restoration goals and to set indicators of progress and endpoints for programmes. However, the model of comparing restored sites to reference sites rarely considers expected variation between sites (White & Walker 1997; but see Mitchell et al. 1999). In addition, such evaluations often focus on overall indicators of a community, even when stated goals include restoration of habitat for focal species (Pavlík 1996). The method in the present study was to estimate quantitatively how important resources needs for a focal species by comparing a range of sites (Schultz & Drulgoch 1999) and to use these estimates to assess habitat restoration efforts. Carlsten, Menke & Pavlik (2000) also suggest that assessment of habitat restoration efforts should depend on essential habitat requirements of focal species, not overall measures such as biomass or biodiversity.

This experiment provides the groundwork on which to base large-scale habitat restoration for Fender’s blue butterfly and has several implications for restoration of rare species’ habitats. First, the research emphasizes the importance of conducting restoration efforts at multiple sites, which can help to generalize potential restoration techniques across the range of habitats for a focal species. Second, as observed by Carlsten, Menke & Pavlik (2000), an experimental approach is extremely useful in determining strategies to restore habitat for rare species. Third, the research suggests a method to link resource needs of rare species to restoration of their habitats. We will be most successful in our restoration efforts when we provide adequate resources for all stages of the life cycle of focal species. In this case, we know we must provide sufficient soil conditions to provide a nectar supply for adult butterflies. But we cannot assist this butterfly’s recovery until we can also find reliable ways to establish larval host-plants at the same site.

Acknowledgements

I thank Ed Alverson of The Nature Conservancy (TNC) and Jock Beall of the Bureau of Land Management (BLM) for suggesting and supporting this project.
References


Received 22 September 2000; revision received 24 May 2001