# The Role of Disturbance in Habitat Restoration and Management for the Eastern Regal Fritillary (*Speyeria idalia idalia*) at a Military Installation in Pennsylvania

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## ABSTRACT

We observed and manipulated habitat for a remnant population of the eastern regal fritillary (*Speyeria idalia idalia*), at Fort Indiantown Gap, an Army National Guard installation in Pennsylvania. Three years of study indicate that the key elements of regal fritillary habitat (larval host plants, adult nectar sources, and adult resting sites) depend on severe disturbance to soils and vegetation. Army training activity (military tracked vehicles and fire) maintained populations of larval host plants (violets) more effectively than combinations of light soil scarification, mowing, and removal of mowed biomass. In addition, plantings of nectar species (milkweeds and thistles) grew best on wetter sites after applying a non-selective herbicide (glyphosate), although herbiciding may be unnecessary on uplands. Because the required larval food and adult nectar and resting sites persist only with recurring disturbance, a practical, biologically effective, and essentially permanent program of disturbance is needed to sustain the population at Fort Indiantown Gap.


**Keywords:** *Asclepias*, *Cirsium*, eastern regal fritillary, endangered species, Pennsylvania, *Speyeria idalia idalia, Viola sagittata*

The regal fritillary (*Speyeria idalia,* Nymphalidae)—a showy reddish-orange and black butterfly with a wingspan up to 4.4 inches (11 cm) (Williams 2001b)—once occupied grasslands from the Canadian Maritimes to the southern Appalachians and west to the Rocky Mountains. In the late twentieth century, its range contracted severely and populations declined, especially east of Illinois (Swengel 1993). Recent morphological and DNA analyses led to the recognition of two subspecies—*S. idalia idalia* in the eastern United States and *S. idalia occidentalis* in the Midwest and West (Williams 2001a, 2001b).

The only known population of the eastern regal fritillary is at Fort Indiantown Gap, Pennsylvania. The population survives on land used for decades for infantry, armored-vehicle, artillery, and aircraft training. The land, roughly 2,800 acres (1,100 ha) of grassland, is dominated by native plants and is subject to soil disturbance and occasional fires. The only other known occurrence of the regal fritillary in the eastern United States is also on a military installation—the Radford Army Ammunition Plant in western Virginia (Derge and Chazal 2000). However, molecular evidence suggests that the Radford population is likely the western regal fritillary (J. Weintraub, Academy of Natural Sciences of Philadelphia, pers. comm.).

The regal fritillary requires food for larvae (Figure 1), nectar for adults (Figure 2), and resting sites for adults (Barton 1996, Kelly and Debinski 1998). At Fort Indiantown Gap, the main larval host species is arrow-leaved violet (*Viola sagittata*), which grows on disturbed and compacted soil but is sensitive to shade and taller competitors. We observed adults feeding on common milkweed (*Asclepias syriaca*), butterfly milkweed (*A. tuberosa*), field thistle (*Cirsium discolor*), and pasture thistle (*C. pumilum*). We flushed resting adults from the shade of low-growing bushy plants or dense grasses, especially from the dominant little bluestem (*Schizachyrium scoparium*), but also from broomsedge (*Andropogon virginicus*), deertongue (*Dichanthelium clandestinum*), goldenrod (*Solidago* spp.), sweet-fern (*Comptonia peregrina*), and brambles (*Rubus* spp.). Because the required larval food and adult nectar and resting sites persist only with recurring disturbance, a practical, biologically effective, and essentially permanent program of disturbance is required to sustain the population at Fort Indiantown Gap. Actually rescuing the eastern regal fritillary from extinction would require reestablishing butterfly

*Ecological Restoration* Vol. 25, No. 2, 2007
ISSN 1522-4740 E-ISSN 1543-4079

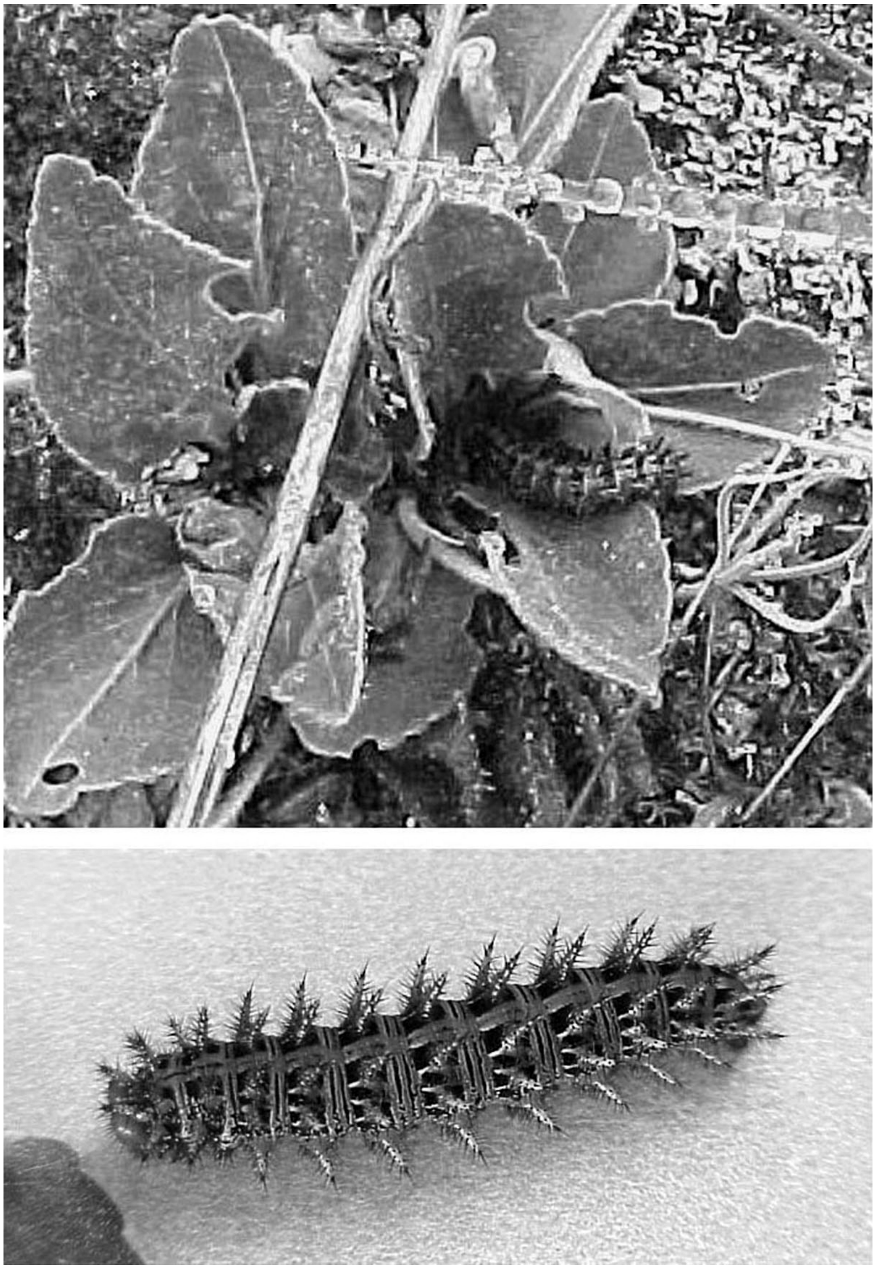

**Figure 1. Eastern regal fritillary larva feeding on arrow-leaved violet (*Viola sagittata*) foliage.**
Photos by Peter Mooreside

populations and sustaining habitat at several other sites.

We evaluated several methods of maintaining or restoring habitat for the regal fritillary while testing five hypotheses: 1) pretreatment by a single mowing in fall to a height of 4 inches (10 cm) would increase survival of planted nectar species; 2) pretreatment by herbiciding one time in fall would increase survival of planted nectar species; 3) lightly scarifying (raking) the ground surface after mowing plus removing cut material would increase violet density; 4) aggressive scarification using military tracked vehicles would increase violet density; and 5) burning would increase violet density.

## Materials and Methods

### *Study Area*

Our study focused on three grassland areas within Fort Indiantown Gap with relatively dense subpopulations of adult regal fritillaries. The sites included 35, 55, and 77 acres (14, 22, and 31 ha) within a 2,800-acre (1,100-ha) area. The Nature Conservancy, in partnership with the Pennsylvania Department of Military and Veterans Affairs, began managing the three areas in the mid-1990s. We used two nearby grassland areas for additional comparisons; they were roughly 42 and 49 acres (17 and 20 ha) in size, and the vegetation, soils, topography, and recent disturbance history were similar to the focus areas. For several years prior to our study, a few regals were seen in each comparison area; after completion of the study, regal fritillaries increased in abundance in the larger area (see Discussion).

### *Enhancing Nectar Species (Experimental Pretreatment with Herbicide or Mowing Followed by Planting)*

In each focus area, we chose subareas that were similar in slope, aspect, soil type (Kunkle et al. 1972, Holzer 1981), and bedrock geology (Berg and Dodge 1981, Geyer and Wilshusen 1982). We then randomly located a cluster of eight plots in an upland position and another cluster of eight plots in a nearby swale (10 to 60 m away) and marked all sixteen 2-m × 2-m plots (rebar stakes). Plots were about 0.5 m apart within a cluster. In each cluster of eight plots, we randomly selected two plots for herbiciding with glyphosate (Rodeo; 2.7 percent foliar application in mid-August 2000 and again two weeks later using 3.3 percent glyphosate). Two other randomly selected plots were mowed in early August to a height of 4 inches (10 cm) and the other four were left intact. Then, in spring 2001, we planted equal numbers of common milkweed, butterfly milkweed, and field thistle in each herbicide-treated and mown plot and in two of the four intact plots at an overall density of roughly 1 plant/ft$^2$ (11 plants/m$^2$). Planting stock was greenhouse-grown from seeds collected in the wild at Fort Indiantown Gap. In late summer-early fall 2002, we counted the number of stems of each

**Figure 2. Eastern regal fritillary adult feeding on common milkweed (*Asclepias syriaca*) nectar.**
Photos by Fred Habegger

**Figure 3. Training activity by an M113 armored personnel carrier in eastern regal fritillary habitat at Fort Indiantown Gap.**
Photos by Roger Latham

nectar species and rosettes of violets and estimated percent cover of every plant species in each plot. Data were averaged for the two replicate plots within the upland or swale position. Because of low sample size and the use of nonparametric statistics, we did not conduct post-hoc pairwise comparisons among treatments.

### *Maintaining Larval Food Plants (Scarifying + Mowing and Mowing + Removal of Biomass)*

In each focus area, we randomly located and marked (rebar stakes) four 5-m × 5-m treatment plots that were similar in slope, aspect, soil type, and bedrock geology. Three of the plots were lightly scarified and de-thatched with a York rake (manufactured by York Modern Corporation, Unadilla, New York), a wheeled, tractor-drawn assembly with a 7.9-ft (2.4-m) wide array of curved steel teeth set 0.75 inches (1.9 cm) apart. We mowed a randomly chosen raked plot in the early growing season and left the cut material lying on the ground. A second plot was mowed and the cut biomass was disposed of off-site, and the third was not mowed. The fourth plot was left intact—neither raked nor mowed—as a control. In late summer-early fall of 2000, 2001 and 2002, we recorded the density of rosettes of violets and percent cover of every plant species in four randomly located, staked, 1-$m^2$ quadrats within each plot and the percent cover of every woody species per plot.

### *Military Light Training Activity (+ Tracked Vehicle)*

In each study area, two adjacent 5-m × 5-m treatment plots were randomly located and marked (rebar stakes) where slope, aspect, soil type, and bedrock geology were similar. In one plot in each pair, the soil was scarified and compacted on 24 August 2000 using multiple, slow passes by a tracked, M113 armored personnel carrier (Figure 3) weighing approximately

Table 1. Species quantified in experimental plots. Nomenclature follows Rhoads and Block (2007).

| Taxon | Group | Origin | Life form |
|---|---|---|---|
| MEAN COVER ≥ 10 PERCENT | | | |
| Poaceae spp., unidentified seedlings | misc. grass | unknown | unknown |
| *Rubus flagellaris* and *Rubus* spp., unidentified seedlings | woody | native | shrub |
| *Schizachyrium scoparium* | dense-foliage grass | native | perennial |
| *Solidago* spp. (*S. gigantea*, *S. juncea*, *S. nemoralis*, *S. puberula*, *S. rugosa*) and *Euthamia graminifolia* | misc. forb | native | perennial |
| MEAN COVER ≥ 1 PERCENT AND < 10 PERCENT | | | |
| *Achillea millefolium* | misc. forb | introduced | perennial |
| *Andropogon virginicus* | dense-foliage grass | native | perennial |
| *Centaurea stobe* ssp. *micranthus* | misc. forb | introduced | biennial |
| *Comptonia peregrina* | woody | native | shrub |
| *Dichanthelium clandestinum* | dense-foliage grass | native | perennial |
| *Potentilla canadensis* and *P. simplex* | misc. forb | native | perennial |
| *Prunus serotina* | woody | native | tree |
| *Verbascum thapsus* | misc. forb | introduced | biennial |
| *Vitis* spp., unidentified seedlings | woody | native | liana |
| MEAN COVER < 1 PERCENT | | | |
| *Viola sagittata* and *Viola* spp., unidentified seedlings | larval host plant | native | perennial |
| *Cirsium discolor* | nectar plant | native | biennial |
| *Cirsium pumilum* | nectar plant | native | biennial |
| *Apocynum* spp., unidentified seedlings | nectar plant | native | perennial |
| *Asclepias syriaca* | nectar plant | native | perennial |
| *Asclepias tuberosa* | nectar plant | native | perennial |
| 13 species | misc. forb | native | annual or biennial |
| 37 species | misc. forb | native | perennial |
| 7 taxa (specimens identifiable to genus or family only) | misc. forb | unknown | unknown |
| 9 species | misc. forb | introduced | annual or biennial |
| 11 species | misc. forb | introduced | perennial |
| 6 species | misc. grass | native | perennial |
| 1 species | misc. grass | introduced | annual |
| 9 species | woody | native | shrub or liana |
| 10 species | woody | native | tree |
| 3 species | woody | introduced | shrub or liana |

11 Mg, making sure that the tracks impacted the entire area of the plot. The other plot was left intact as a control. In late summer-early fall 2000, 2001 and 2002, we recorded the density of rosettes of violets and percent cover of every plant species in four randomly located, staked, 1-$m^2$ quadrats in each experimental plot and the percent cover of every woody species over each entire plot.

### Data Analysis: Experiments

To test for treatment effects, we summed cover by groups of species classified by ecological function, life form, native or introduced (Table 1). We used nonparametric Kruskal-Wallis analysis of variance and the median test for experiments with one independent variable, and the Scheirer-Ray-Hare extension of the Kruskal-Wallis test for two independent variables with an interaction effect (StatSoft 1994, Sokal and Rohlf 1995). The experiment-wise Type I error rate was adjusted using the Dunn-Šidák method (Sokal and Rohlf 1995). In either test, treatments or controls were considered to differ significantly in their effects on a variable if $p < 0.05$ and to differ marginally significantly if $0.05 < p < 0.1$.

### Food-plant Surveys

We surveyed food plants in 259 2-m × 2-m quadrats that we located randomly throughout the three focus and two comparison areas (1 quadrat/acre or about 0.4 ha). We counted larval host plants (violets) and nectar species (common milkweed, butterfly milkweed, thistles) as individual rosettes or stems, without attempting to distinguish ramets from genets. We estimated cover as 0 percent, 1 percent, or the nearest multiple of 5 percent for violets, common milkweed, butterfly milkweed, thistles, dense-foliage grasses, other grasses, all other plants, and bare ground. Violets were surveyed in late spring 2001 and nectar plants in fall 2001, along with cover of other plant categories and bare ground. Contrasts between the main study areas and the comparison areas were tested using Kruskal-Wallis

**Table 2. Results of nectar species planting experiment two years after planting. Median responses to herbicide treatment are given by landscape position (numbers in parentheses) for several variables in which the numerical response appeared to differ strongly between swales and uplands, although the effect of landscape position was statistically significant only for woody plant cover. NS indicates p > 0.1. Nectar plants are *Asclepias syriaca, A. tuberosa, Cirsium discolor*, and *C. pumilum*; dense-foliage grasses are *Schizachyrium scoparium, Andropogon virginicus*, and *Dichanthelium clandestinum*.**

| treatment → | | | **Herbicided** | | **Control** | | **Intact** | | **Mowed** | |
|---|---|---|---|---|---|---|---|---|---|---|
| landscape position → | | | swale | upland | swale | upland | swale | upland | swale | upland |
| variable | *H* | *P* < | (medians) | | | | | | | |
| Nectar plant density (per m²) | 16.6 | 0.005 | 11.5<br>(12.5) | (10.5) | 0.5 | | 7.2 | | 7.5 | |
| Nectar plant percent cover | 14.8 | 0.001 | 8.0<br>(13.2) | (2.8) | 0.1 | | 2.5 | | 1.1 | |
| Dense-foliage grass percent cover | 6.9 | NS | 2.5<br>(2.5) | (0.2) | 40.2 | | 30.2 | | 22.5 | |
| Percent of bare ground | 10.1 | 0.025 | 31.2<br>(17.5) | (32.5) | 3.0 | | 5.4 | | 6.5 | |
| Woody plant percent cover | 6.7 | 0.1 | 8.5 | 3.0 | 38.5 | 8.2 | 50.8 | 7.8 | 30.5 | 3.0 |
| Woody plant landscape position | 6.2 | 0.025 | | | | | | | | |
| Introduced species percent cover | 3.7 | NS | 7.8<br>(7.0) | (8.5) | 2.0 | | 2.5 | | 7.6 | |

analysis of variance and the median test.

### *Comparing Burned/ Unburned Areas*

A wildfire burned a portion of one focus area on 31 October 2000. We assessed effects on larval host plants by sampling six randomly placed quadrats in the burned area, each paired with a nearby quadrat in the adjacent unburned area. The six pairs of quadrats spread across about 10 acres (4 ha). We undertook quantitative comparisons despite the lack of treatment randomization and true replication (Van Mantgem et al. 2001). We surveyed quadrats at the same time and with the same methods as in the food-plant survey. We compared the burned and adjacent unburned area using Wilcoxon's signed-ranks test, also known as the sign test, a nonparametric analog to the *t* test for dependent or paired samples (StatSoft 1994; Sokal and Rohlf 1995). Error estimates throughout the text are SE.

## Results

### *Enhancing Nectar Species*

One year after planting, field thistle cover with herbicide pretreatment was greater than that without pretreatment, especially in swales where it was six to seven times greater. Pretreatment mowing resulted in less than half of the field thistle cover that occurred in control plots. Cover of the two planted milkweed species and survival of all three planted species were similar in the first growing season. Herbiciding reduced woody plant cover, resulting in less than ten percent of the woody plant cover in control and intact, planted plots. However, herbiciding also reduced the cover of the dense-foliage grasses—important resting sites for adult regals—to less than five percent of the cover in control and intact, planted plots. Native species cover overall was reduced more than tenfold, and introduced species as a proportion of total cover increased more than 12 times relative to control and intact, planted plots. Violets were present in too few plots to analyze their density and cover responses.

Two years after planting, differences among site preparation treatments and landscape position remained significant (Table 2). Pretreatment with glyphosate slightly increased densities of surviving nectar plants in upland and swale plots but substantially increased their cover in swales only, where nectar plants attained 5 to 12 times their cover in other planted plots. Herbiciding reduced the cover of woody plants more than mowing in swales but not in uplands. Mowed planted plots did not appear to differ from intact planted plots in any of the response variables.

### *Maintaining Larval Food Plants*

Our low-impact experimental manipulations provided no significant differences among treatments and controls in any response variable for any of the three growing seasons.

### *Military Light Training Activity*

Sample size was inadequate to show significant differences among treatments and controls, but several variables suggested trends (Table 3). For example, two growing seasons after the

**Table 3. Results of light military training experiment. Asterisks indicate where treated plots differed marginally significantly from control plots (median test $\chi^2 = 6.0$, unadjusted p = 0.014, adjusted p ≈ 0.10). Violets are *Viola sagittata*; nectar plants are *Asclepias syriaca, A. tuberosa, Cirsium discolor*, and *C. pumilum*; dense-foliage grasses are *Schizachyrium scoparium, Andropogon virginicus*, and *Dichanthelium clandestinum*.**

| Variable | Years after treatment | Tracked (median) | Control |
|---|---|---|---|
| Violet density (per m²) | 1 | 0.62 | 0.25 |
| | 2 | 4.00 | 0.50 |
| | 3 | 2.25 | 0 |
| Violet percent cover | 1 | 0.25 | 0.12 |
| | 2 | 0.62 | 0.12 |
| | 3 | 0.38 | 0 |
| Nectar plant percent cover | 1 | 0 (mean 0.08) | 0 (mean 0) |
| | 2 | 0.25* (mean 0.58) | 0* (mean 0) |
| | 3 | 0 (mean 0.08) | 0 (mean 0) |
| Dense-foliage grass percent cover | 1 | 5.00* | 28.75* |
| | 2 | 19.69 | 36.25 |
| | 3 | 18.38 | 50.00 |
| Bare ground percent cover | 1 | 30.00* | 4.50* |
| | 2 | 16.88 | 1.88 |
| | 3 | 7.88 | 10.00 |
| Annual/biennial percent cover | 1 | 0.16 | 0.12 |
| | 2 | 0.69 | 0 |
| | 3 | 0.25* | 0* |
| Woody plant percent cover | 1 | 11.56 | 5.00 |
| | 2 | 7.50 | 10.00 |
| | 3 | 27.50 | 10.00 |
| Introduced species percent cover | 1 | 2.66 | 5.25 |
| | 2 | 0.62 | 0.62 |
| | 3 | 0.12 | 0.50 |

tracked-vehicle activity experiment, violet cover and density appeared to be higher in tracked-vehicle-scarified plots than in controls. By the third growing season, violets had disappeared from control plots but persisted at low numbers in treated plots. Tracked-vehicle activity, even without planting, appeared to increase field thistle cover and total cover of all milkweed and thistle species relative to controls. Tracked-vehicle activity increased bare soil, but cover matched that of the control plot in the third year. Dense-foliage grasses considered important as cover for adult regal fritillaries appeared to diminish in treated plots compared with controls but showed signs of recovery two to three years after treatment.

### Comparing Burned/ Unburned Areas

Six months after the fall wildfire, we found higher densities of violets in the burned area (mean difference, in rosettes per m²: 7.75 ± 2.38; Z = 2.04, p = 0.04), lower total plant cover (mean difference, in percentage points: 25.6 ± 3.44; Z = 2.04, p = 0.04), and a higher percentage of bare ground (mean difference: 25.0 ± 5.33; Z = 2.04, p = 0.04). One year later, none of these variables differed significantly between the burned and the unburned areas.

### Food-plant Surveys

In the spring survey, violet densities were similar in habitat that was densely populated by adult regal fritillaries (n = 3: 2.9 rosettes per m² ± 0.55) but less dense in nearby, similar habitat with fewer regals (n = 2: 3.4 ± 2.02). We estimated that 1.8 million violets were present in the main study areas and 1.3 million in the comparison areas. Focus areas had significantly lower plant cover than comparison areas (mean total percent cover, respectively: 77 ± 6.5, 94 ± 0.23; median test $\chi^2$ = 5.00, d.f. = 1, p = 0.03). This effect was driven mainly by non-grasses, which also differed significantly (mean percent cover, respectively: 26 ± 3.9, 42 ± 0.9; median test $\chi^2$ = 5.00, d.f. = 1, p = 0.03). In the spring survey, bare ground was higher (marginally significant) in the focus areas than in the comparison areas (mean percent cover, respectively: 19 ± 3.9, 9 ± 2.3; Kruskal-Wallis $H_{(1,5)}$ = 3.00, p = 0.08). None of the other measured variables differed between focus and comparison areas.

In the fall survey, nectar plants had similar densities among the focus areas (0.08 stems per m² ± 0.06) and two comparison areas (0.04 ± 0.05). Although sparse and patchy, total populations were estimated at 3,100 common milkweeds, 34,000 butterfly milkweeds, and 87,000 thistles in study areas; there were no milkweeds and 39,000 thistles in comparison areas. In the fall survey, focus areas had significantly less bare ground than comparison areas (mean percent cover, respectively: 5.4 ± 1.8, 8.2 ± 0.01; median test $\chi^2$ = 5.0, d.f. = 1, p = 0.03). None of the other measured variables differed significantly between the two sets of grasslands.

## Discussion

Habitat that was densely populated by eastern regal fritillaries differed from nearby, similar habitat with fewer regals, not in larval food-plant density as we expected, but in having 80 percent of the plant cover and 66 percent of the cover of plants other than grasses in the spring (there was no difference in the fall). The data suggested (inconclusively) that nectar plant densities were also higher where regals were more abundant. Three years following the fieldwork, however, one of the comparison areas heavily used for military training and formerly nearly devoid of regals became as densely populated with adults as the three focus areas (from unpublished data from co-authors B. Ferster and P. McElhenny). We hypothesize a lag time for regal fritillaries to colonize an area after major disturbance; however this does not explain the dense adult populations in areas of sparser plant cover in spring.

The wildfire boosted violet densities in the first year, in part, by decreasing plant cover. Tracked-vehicle light training activity decreased plant cover for two years and perhaps increased violet density and cover for three years, with the largest effect occurring in the second year. Effects of the fall wildfire were only detectable for one growing season.

While fire and tracked-vehicle activity did enhance food plants, they temporarily decreased the extent of grasses with dense foliage (little bluestem, broomsedge, deertongue). We infer from frequent flushing of adult regal fritillaries that these grasses provide important cover and resting sites. Thus, disturbance should be patchy to maintain all key components of habitat in close proximity. That is, aggressive disturbance methods should be used on a small proportion of the area in any one year and in scattered patches to create a mosaic of post-disturbance successional stages and thereby sustain regal fritillaries.

In the nectar-species experiment, mowing was less effective than no pretreatment in enhancing target species. Herbicide application suggested two advantages: it fostered the growth of native thistles and reduced woody plant invasion. However, it also facilitated introduced herbaceous species, including known invasives such as spotted knapweed (*Centaurea stobe* ssp. *micranthus* = *Centaurea maculosa*). Introduced species cover apparently declined to insignificant levels in the second growing season after herbicide use. However, this result might be weather-related. Research on the use of herbicide as a pre-planting site-preparation tool in areas with moist soil should continue as part of an adaptive management program.

Our attempt to foster violets using low-impact methods was ineffective. York-rake light scarification followed by either mowing and removing cut material, mowing and leaving cut material on the ground, or not mowing at all had no effect on violet density or cover or on any other vegetation measure. In contrast, scarification by a modest amount of tracked-vehicle activity substantially increased the density and cover of violets and promoted a modest increase in cover of the native plants considered to have the greatest value as nectar sources for adult regal fritillaries. Light training activity and wildfire seemed to increase density and cover of regal fritillary larval host plants, but these effects were short-lived, demonstrating the necessity for patchy disturbance that is more frequent or more severe, or both, to maintain eastern regal fritillary habitat in the long term.

The western regal fritillary and other rare butterfly species are also dependent on disturbance. Swengel (1996) found that regals and most other prairie specialist butterflies are more abundant in habitat that is mowed, hayed, or grazed than in those managed by burning. However, in a few cases, areas in the American Midwest that are managed with fire support "relatively high densities" of regals (Swengel and Swengel 1997). Swengel (1997) determined that in all of the areas she studied, "*S. idalia [occidentalis]* was significantly more abundant in larger prairie [remnants] with topographic diversity and management by haying or grazing." Swengel (1998) found that most grassland specialists, including the western regal fritillary, showed "significant effects from management, typically favoring less frequent and/or less intrusive management." In Iowa, Debinski and Kelly (1998) found that prairie violet (*Viola pedatifida*) densities were highest in moderately grazed and recently burned prairies and that violet density correlated significantly with grazing intensity but not with mowing or burning in the absence of grazing.

Results have been somewhat mixed but often positive on the use of fire as a butterfly habitat management tool (Swengel 2001, Panzer 2002). Part of the reason for the inconsistency is that interpreting burning effects depends strongly on the scale of observation, in both space and time. In the area directly affected by a prescribed burn, prairie specialist butterflies typically decline sharply and full recovery takes one to five years (Swengel 1996, Panzer 2002). However, after the burn, the recovered population often grows larger (Schultz and Crone 1998). The picture changes when observations are integrated across an entire habitat "island" and certain conditions prevail, namely that just a fraction of the habitat is burned in any one year, successive fires occur in different areas within the habitat, and several years elapse between fires. The post-fire decline may be only a small fraction of the total population, and fire may increase an entire population's density when averaged over the long term. For example, habitat for the endangered Fender's blue butterfly (*Icaricia icariodes fenderi*) improved with burning (Schultz and Crone 1998), which removed invasive weeds and increased oviposition rates per female, presumably by allowing greater growth of perennial lupines (*Lupinus arbustus, L. sulphureus* ssp. *kincaidii*), the larval host plants. Although eggs and larvae were killed locally by fire, burning small areas had a positive impact on overall populations of Fender's blue.

The investigators recommended burning an average of one-third of the habitat area per year (Schultz and Crone 1998).

Panzer (2002) tracked 151 species in seven orders and found that 93 percent had consistent short-term responses to prescribed burning among populations and sites; 26 percent increased and 40 percent declined. Mean recovery time for 163 insect populations representing 66 species was 1.32 years (sd = 0.47). In 84 percent of cases, recovered population sizes exceeded those on unburned tracts. Panzer (2002) determined that three attributes—remnant dependence (obligatory association with remnants of fragmented ecosystems), preference for upland habitats, and low vagility (capacity or tendency to move about or disperse)—were significant predictors of negative response to fire. The regal fritillary has been described as having a high apparent degree of remnant dependence (Panzer et al. 1995). It inhabits uplands, lives in the duff in the larval stage, has low vagility during its larval stage, and is univoltine, thus falling solidly into the "presumed hypersensitive" category. It is reasonable to assume hypersensitivity to disturbances besides fire that have a strong impact on the duff and the organisms that live in it, including military training activity.

The precariousness of the eastern regal fritillary and the importance of the sole known population (Fort Indiantown Gap) cannot be overstated. We suggest that managers use extreme caution while testing and evaluating disturbance type, extent, frequency and severity in the quest for a management regime of overall benefit to all life stages of the eastern regal fritillary. There is little doubt that some level of military training activity is conducive to the maintenance of regal habitat at Fort Indiantown Gap. However, there are still large gaps in our knowledge that make it prudent to exercise the utmost caution in planning any resumption of such activity in the core habitat areas.

Elements of the impact of training activity that are potentially crucial, but still poorly known, include the effects of seasonal timing of training activity; the length of rest period between successive training periods at the same site (and interaction of this effect with soil moisture availability, soil parent material, slope and aspect); the location of training activity relative to larval feeding areas, pupation sites, nectaring areas, and egg-laying sites; the intensity or severity of training activity; and interactions among all these factors. The eastern regal fritillary's future may well depend on further experimental work to clarify these issues.

## Acknowledgments

We are grateful to the Pennsylvania Department of Military and Veterans Affairs for cooperation and assistance and to the U.S. Department of Defense, National Guard Bureau, which funded this study and provides ongoing funding for habitat restoration and management for the regal fritillary at Fort Indiantown Gap. For advice, assistance with experimental treatments, and data collection and processing, we thank Susan Brockman, Jessica Coster, Dr. Greg Eckert, John Fronko, Jan Getgood, George Gress, Fred Habegger, Chuck Hill, Dana Hornyak, Joe Hovis, John Kasitz, Joe Kern, Jessica Kindt, Richard Light, David McNaughton, Rose Petrunyak, Jen Sale, Jean Sellers, Glenn Stauffer, Mark Swartz, Richard Voytko, Dr. Jason Weintraub, and Cory Zimmerman. We also thank Ernst Conservation Seeds, Meadville, Pennsylvania, for donating plants for the nectar species planting experiment.

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