

## THE EFFECTS OF A FALL PRESCRIBED BURN ON *HEMILEUCA EGLANTERINA* BOISDUVAL (SATURNIIDAE)

PAUL M. SEVERNS<sup>1</sup>

U.S. Army Corps of Engineers, Willamette Valley Projects, Box 429, Lowell, Oregon 97452, USA

**ABSTRACT.** Autumn prescribed burning is often used to manage a rare wet prairie plant community endemic to the Willamette Valley in western Oregon, USA. A local race of day flying Saturniid moth, *Hemileuca eglanterina*, was used to investigate the effects of a prescribed burn on adult, larval, and egg mass abundance contrasted with an adjacent unburned area. Adult male moths were not more frequently encountered in the burned habitat but female *H. eglanterina* laid more than twice as many egg masses in the burned compared to the unburned habitat in the burn year. Furthermore, females laid significantly more egg masses on the burn edge in the burn year ( $p < 0.001$ ), suggesting that *H. eglanterina* chose to oviposit on burned host plants over unburned host plants. Egg masses laid before the prescribed burn did not survive the fall fire, demonstrating that the management practice is catastrophic for the immature population. Although fire can substantially reduce immature Lepidoptera populations, some species living in ecosystems that had a frequent historic fire return interval may benefit from the ecological release caused by a prescribed burn. Fires consuming entire habitat parcels of fragmented ecosystems may lead to population bottlenecks and an increased frequency of inbreeding. Conservative prescribed burning practices with unburned refugia may be the most effective way to manage for the conservation of rare grassland plant communities and their insect fauna.

**Additional key words:** fire, grasslands, maternal investment, fire-adaptation, buckmoth.

Many grassland ecosystems historically experienced wild or anthropogenic fires that maintained floral structure and community composition (Vogl 1974). Grasslands the world over have suffered substantial reductions in area from urbanization, agricultural development, habitat fragmentation, and successional change following the suppression of wildfires. Prescribed burning is frequently employed to manage grasslands for rare plants and maintain a primarily herbaceous plant community by restoring a past ecological process (Leach & Givnish 1996, Pendergrass et al. 1998a, b). Fires, prescribed or wild, are generally catastrophic for immature insects that live above or near the ground level (Fay & Samenus 1993, Schultz & Crone 1998) and may also kill adult insects that are weak fliers (Morris 1975, Panzer 1988). The effect of prescribed burning on insect abundance often differs between insect families and even among individual species of the same genus (Crawford & Harwood 1964, Cancelado & Yonke 1970, Bertwell & Blocker 1975, Evans 1984, Benzie 1986, Siemann et al. 1997, Blanche et al. 2001, Panzer & Schwartz 2001), suggesting that some species benefit from fire while others do not. Lepidoptera communities also appear to have fluctuating or unpredictable adult abundance between burned and unburned treatments (Swengel 1996, 1998, Fleishman 2000, Panzer & Schwartz 2001), intimating that Lepidoptera response to fire may be species specific.

Swengel (1998), Panzer and Schwartz (2001), and Siemann et al. (1997) all mention that prairie inhabiting insects, especially prairie endemics, are likely to be adapted to cope with fires. I investigated the effects of a prescribed burn on *Hemileuca eglanterina* Boisduval

(Saturniidae), a dayflying moth of western North America, which occupies a unique wet prairie ecosystem in the Willamette Valley of western Oregon, USA. Historically, the Willamette Valley was burned on nearly an annual basis by Native Americans to increase native food crops and aid in hunting (Boyd 1986). Wet prairie fires are typically low intensity and burn quickly over the grassland consuming the low levels of available fuel (pers. obs.), which is generally true for most grasslands (Agee 1993). Translocation of heat from a wet prairie burn rarely reached soil depths >6.0 cm (Pendergrass 1995). Because of the historical role that anthropogenic fires had in maintaining the Willamette Valley prairie flora, autumn prescribed burns are employed to manage the remnant prairie plant communities (Pendergrass et al. 1998b). The effect of prescribed burning on the floral community has been studied intensively by Pendergrass (1995) and Taylor (1999), but the consequence of fall fires on wet prairie insects has not yet been investigated.

I chose *H. eglanterina* as a study species because: (1) it lays eggs in masses that are conspicuous (Fig. 1a); (2) it is monophagous at the study site; and (3) the local race of *H. eglanterina* appears to be ecologically and temporally restricted to the wet prairie. Temporal difference in flight times of two to three weeks and elevation separates the wet prairie from the montane moth populations. Moreover, the wet prairie populations appear to be ecologically restricted to the wet prairie because I have not located *H. eglanterina* in the nearby oak woodlands, upland prairie, or riparian areas surrounding occupied wet prairie sites. *H. eglanterina* are considered polyphagous throughout their range, accepting host species from the Salicaceae, Rosaceae, Rhamnaceae, and Aceraceae (Ferguson 1971), but use only *Rosa nutkana* in the wet prairie,

<sup>1</sup> Current address: Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331, USA. Email: severnsp@science.oregonstate.edu



FIG. 1. Immature lifestages of wet prairie *H. eglanterina*. **a**, Egg mass laid on the apical end of *Rosa nutkana*; **b**, A group of late 2nd and early 3rd instar larvae.

despite the presence of other reported larval host species (pers. obs.).

Owing to a frequent historical fire return interval in the Willamette Valley, it is possible that native wet prairie Lepidoptera have developed adaptations related to fire survival and behaviors that exploit vacant ecological niches created by the fire. This paper reports the behavioral and life history response of *H. eglanterina* to a fall prescribed burn that bisected a wet prairie moth population. I monitored the adult, larval, and egg populations to describe the demographic differences of each life stage in the burned and unburned habitat. Specifically, I tested the hypothesis that *H. eglanterina* adults were differentially attracted to burned prairie and that egg masses were adapted to fire survival.

#### MATERIALS AND METHODS

**Study site.** Willamette Valley wet prairie is a seasonally inundated grassland ecosystem currently exist-

ing in fragments that total <1% of its historical expanse. Due to the sizable loss of habitat, Willamette Valley wet prairie represents one of the most endangered ecosystems in the U.S. (Noss et al. 1995). The wet prairie ecosystem contains four endemic plant species listed as either threatened or endangered (Oregon Natural Heritage Project 2001), and it is dominated by tufted hairgrass (*Deschampsia cespitosa* L., Poaceae), camas lily (*Camassia quamash* Pursh, Agavaceae), dwarf woolly sunflower (*Eriophyllum lanatum* Pursh, Asteraceae), Hall's aster (*Aster hallii* Cronq., Asteraceae), and nootka rose (*Rosa nutkana* Presl., Rosaceae).

I selected Amazon wet prairie Research Natural Area (RNA), in the southern Willamette Valley approximately 10 km west of Eugene, Oregon, USA (Fig. 2) as the study site because of its relatively large size and the integrity of the native plant community. In October 1998, the U.S. Army Corps of Engineers burned 16.2 ha of a 33 ha wet prairie parcel to control exotic

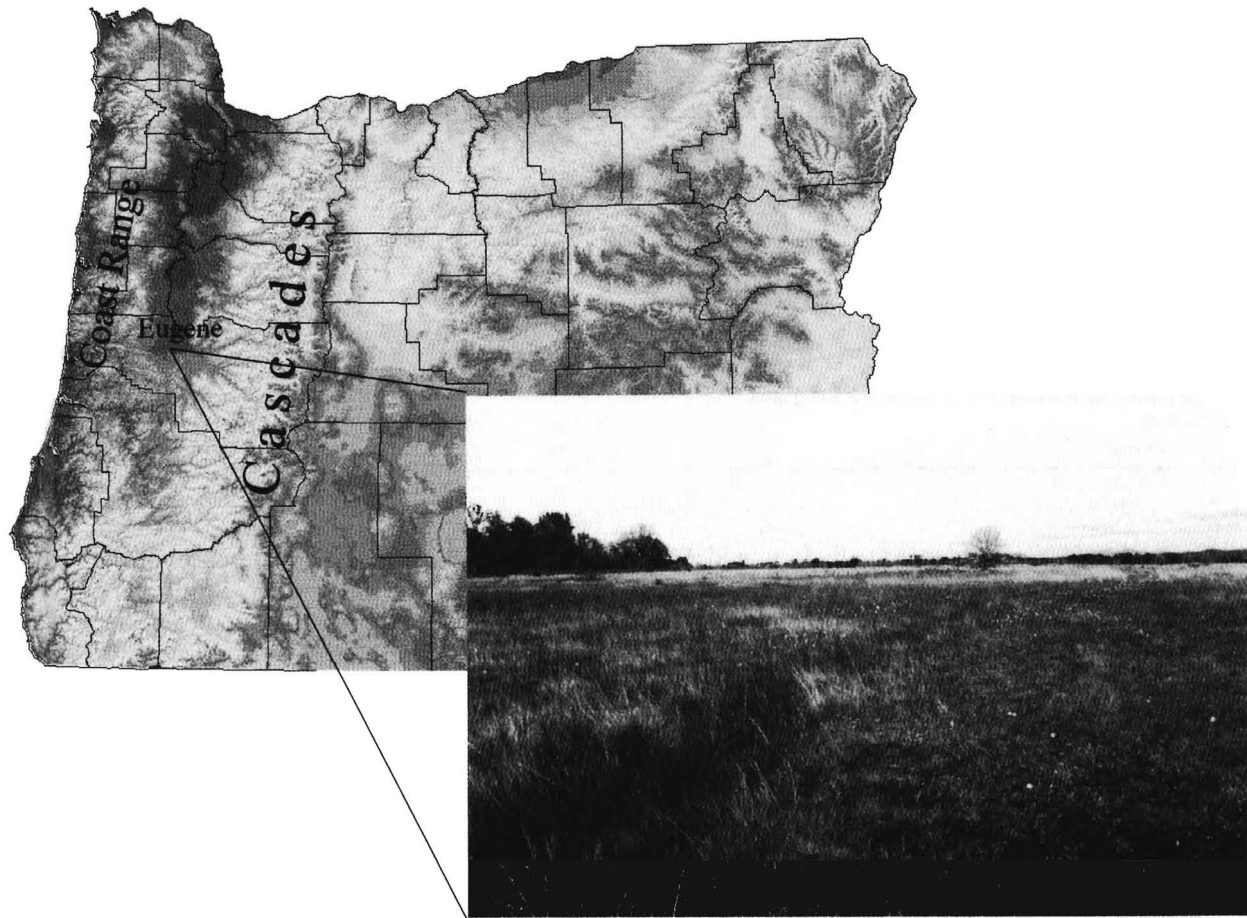


FIG. 2. Map of Oregon and the relative location of the prescribed burn study site. The insert shows the burn edge eight months following the prescribed burn.

plants and encourage the native wet prairie plant community. The other half of the parcel was left unburned.

**Study species.** *Hemileuca eglanderina* is a large, diurnal moth species ranging west of the Rocky Mountains from southern California, USA to southern British Columbia, Canada. Adults fly in early July through the middle of August in the Cascade and Coast Range mountain populations >1500 m elevation, but fly from mid August through late September in Willamette Valley wet prairie ( $\approx 100$  m elevation). Wet prairie *H. eglanderina* oviposit eggs in early September and remain in diapause until the beginning of April. Instars 1–3 are gregarious on *Rosa nutkana* (Fig. 1b) but disperse in the 4th instar. The larvae are armed with urticating spines that can range from mildly irritating to as painful as a honeybee (*Apis mellifera* L., Apidae) sting when pressure is applied to the spines (pers. obs.), which is common in the genus (Ferguson 1971).

**Adult abundance.** To sample adult abundance I

placed two macroplots, each 0.41 ha and marked with 2 m tall metal rebar sections, in the center of the prescribed burn and control treatments. For one hour during the peak flight period, 1100–1400 h, on three separate occasions in two preburn years and the burn year from mid to late August, adult moths flying through the burn and control macroplots were captured and marked on the ventral hindwing with a permanent marker, then released. All adults flying through the macroplots were counted whether they were marked or captured. I used the number of adult fly-throughs as a relative abundance index to identify any adult bias for burned or unburned habitat. In addition to direct adult observations, the location of egg masses with respect to the burn treatment was used as an indicator for the presence of adult female moths.

The burn year is defined as the first calendar year from the time of the burn, October 1998–October 1999, the preburn year as October 1997–September 1998, and the postburn year being from November

TABLE 1. Adult, larval, and egg population data collected from the burned and unburned treatments for *H. eglanderina* in the Amazon RNA study site. \* = significantly different when  $p < 0.05$ .

Demographic measure	Burn treatment	Unburned (control)	Statistical analysis
# of adults observed/macropilot			Chi-square test
Preburn year 1	34	27	Pre1/Pre2 $p > 0.05$
Preburn year 2	39	36	Pre2/Burn $p > 0.05$
Burn year	48	41	Pre1/Burn $p > 0.05$
# of larvae/macropilot			Chi-square test
Preburn year	64	136	Pre/Burn $p < 0.0001^*$
Burn year	0	370	Burn/Post $p < 0.0001^*$
Postburn year	258	185	Pre/Post $p < 0.001^*$
# of egg masses laid on the burn edge			Fisher Exact test
Burn year	10	0	$p < 0.001^*$
Postburn year	1	5	
# of egg masses for the entire burned and unburned area			Chi-square test
Burn year	39	17	$p > 0.05$
Postburn year	34	24	

1999–October 2000. *H. eglanderina* fly from mid August through late September at the study site and laid eggs before the prescribed burn.

**Larval abundance.** To detect larval population differences in the burned and unburned habitat, I directly counted all of the *H. eglanderina* larvae in the two macroplots that were used for the adult sampling. I counted larvae in the first week of May of the preburn, burn, and postburn years.

**Egg mass abundance and fire adaptation.** I searched for egg masses during late April and early May of the burn and postburn years in the entire study site. Line transects approximately 15 m apart were walked throughout the entire burn ( $\approx 16$  ha) and control ( $\approx 16$  ha) areas, inspecting each *Rosa nutkana* plant for early instar larvae. The number of egg masses encountered and the number groups of 1st instar larvae for which no egg masses could be found were combined into a total egg mass census for the burned and unburned areas.

To determine if egg masses were adapted for fire survival, I located five egg masses and followed their fate immediately following the burn. I noted any qualitative differences in the egg masses before and after the burn.

Female preference for oviposition was measured by the number of egg masses laid on the burned or control side of the burn edge. The burn edge (Fig. 2), approximately 500 m long, was sampled  $\pm 30$  m on each side of the edge for the entire length of the burn boundary. The amount of host plant appeared to be more or less equivalent on both sides of the burn edge.

**Adult, larval and egg mass analysis.** The number of egg masses found on the burned side of the edge was compared to the number of masses found on the unburned edge among years and the burn treatment

using a Fisher's exact test. Differences in adult abundance, the number of larvae in each macroplot, and the number of egg masses laid in the burned and unburned areas were assessed among years and between burn treatments by Chi-square tests.

**Host plant response and analysis.** Host plant response to the prescribed burn was measured in the first and second week of June in the burn and postburn year. I estimated *R. nutkana* cover in sixteen 30 m long  $\times$  1 m wide belt transects randomly located in each burn and control macroplot. Cover measurements were made in 1 m<sup>2</sup> subplots for ease and accuracy, then weighted and added together to yield cover for the belt transect. Host plant stature was divided into height classes, 0–25 cm and >25–50 cm, and the cover of each height class was visually estimated to the nearest 1%, for 1–10% cover, and in 5% increments thereafter. *R. nutkana* cover estimations were performed by the author for consistency between and within years. Host plant height class cover differences between treatments (burn vs. control) within years were analyzed using a Mann-Whitney *U*-test. All statistical analyses were performed with the NCSS (2000) statistical package.

## RESULTS

**Adult, larva, and egg mass populations.** Adult abundance did not differ between burned and unburned prairie between the two preburn years and the burn year (Table 1). The number of egg masses censused in the burn year from the burned (16.2 ha) and unburned (16.2 ha) habitats was nearly twice as high in the burned area compared to the unburned area in the burn year (Table 1), suggesting that female moths preferred to lay eggs on burned rose. A similar distribution of egg mass number occurred in the postburn year, however there were no



statistical differences in egg mass number within burn treatments and between years (Table 1). Egg mass number from the burn edge habitat was significantly different ( $p < 0.001$ ) between the burn and postburn year among the burn and unburned edge treatment, indicating that females preferred to oviposit on the burned plants in the burn year (Table 1).

The fire destroyed the five egg masses found immediately following the burn. Many of the eggs appeared to have boiled and then ruptured from the heat of the burn, giving the appearance that they had hatched. Larva number in the burned macroplot of the burn year was lower in the burn year compared to all other years (Table 1), indicating that none of the egg masses laid before the burn produced 1st instar larvae.

**Host plant response.** In the burn year, the amount of *R. nutkana* in the <25 cm height class did not statistically differ between the control and burn plots (mean cover =  $0.22 \text{ m}^2/\text{transect} \pm 0.06$  Mann-Whitney *U*-test  $p = 0.85$ ), but there was significantly more rose from the 25–50 cm height class in the control plot compared to the burn plot (burn =  $0.21 \text{ m}^2/\text{transect} \pm 0.1 \text{ m}^2$ ; unburned =  $0.62 \text{ m}^2/\text{transect} \pm 0.1 \text{ m}^2$  Mann-Whitney *U*-test  $p = 0.018$ ). The postburn year experienced no significant rose quantity differences between treatments in the <25 cm height class (mean cover =  $0.174 \text{ m}^2/\text{transect} \pm 0.05 \text{ m}^2$  Mann-Whitney *U*-test  $p = 0.895$ ) and the 25–50 cm height classes (mean cover =  $0.645 \text{ m}^2/\text{transect} \pm 0.20 \text{ m}^2$  Mann-Whitney *U*-test  $p = 0.11$ ). These comparisons suggest there was more *H. eglanderina* host plant available in unburned areas during the burn year when females laid eggs.

#### DISCUSSION

Adult abundance, measured by the number of individuals observed flying through the macroplots in the burn and unburned areas, was not significantly different between years or the burn treatment (Table 1), arguing against the hypothesis that adult moths prefer recently burned prairie to adjacent unburned prairie. However, females laid more than twice as many egg masses in the burned compared with the unburned prairie during the burn year (Table 1), implying there was a burn bias that was not detected through direct adult observations. Examination of the egg mass placement on the burn edge, where moths were assumed to have made a choice to oviposit between burned or unburned plants, suggested that reproductive effort was directed towards the burned plants in the burn year (Table 1). Maternal preference for the burned area and the burn edge in the burn year supports the hypothesis that female *H. eglanderina* were attracted to the burned area.

The discrepancy between adult and egg mass abundance may be explained by the gender of adult moths surveyed by each method. In the combined 18 hours of adult sampling among the three years, no females were detected. In fact, over the last five years of visiting the study site I observed only three females amongst hundreds of male observations. During the two preburn years and the burn year adult sampling effort, male *H. eglanderina* patrolled the study site in roughly circular flight patterns (presumably searching for females) over large areas of the entire prairie, encompassing both the burned and unburned areas. Since egg mass counts and adult abundance appeared to effectively measure the relative occurrence of the two genders, it is not surprising that the results are inconsistent with each other, especially if there are behavioral differences between genders.

Differences in the effect of prescribed burning on adult abundance and the number of egg masses laid demonstrates the need to sample multiple lifestages within a species to estimate the effects of prescribed burning. For example, if only adult abundance was used to determine the effects of fire, I would have concluded there were no effects on the population. Conversely, if burn affinity was based solely on egg mass number, I could have inferred that adult distribution was biased towards the burn area. Basing the effects of the prescribed burn on larval abundance would have yielded a conclusion that the fire was catastrophic. Many studies often rely heavily on adult abundance to describe the effects of fire on Lepidoptera (Swengel 1996, 1998, Fleishman 2000, Huebschman & Bragg 2000, Panzer & Schwartz 2001). However, in this study direct adult *H. eglanderina* observations yielded a non-significant treatment response (Table 1), suggesting that adult observations of vagile lepidopterans may not be adequate to assess the effects of fire on study populations. Sampling all lifestages and monitoring abundance may narrow the variability of results in any community study, but measuring abundance of multiple lifestages is time consuming. Perhaps focusing on a subset of specialist, generalist, widely distributed, and locally restricted species may yield generalizable trends concerning the effects of fire on Lepidoptera natural history, conservation, and community response.

Although *H. eglanderina* egg masses showed no evidence of being resistant to fire, there may be an advantage to insect species that colonize recently burned areas in an ecosystem that experiences frequent fires. Larvae feeding on plants in a burned area may experience higher quality food (McCullough & Kulman 1991, Stein et al. 1992) which could result in a rapid

population size increases if survivorship and fecundity is increased by food quality. Recently burned habitat should also have a number of exposed niches, from fire induced mortality on immature insects, that can temporarily be exploited by opportunistic species. Furthermore, females choosing to oviposit in a burned area may impart increased survival to their progeny. A recently burned area would tend to have a low fuel load than an area that has not been burned, resulting in a fire that is not as hot as the original one, and perhaps increased survival of egg masses. Two egg masses that produced numerous 1st instar larvae were found on the burn edge where the fire was extinguished, suggesting egg masses may be resilient to slightly elevated temperatures above the ambient.

**Lepidoptera conservation and prescribed burning.** The number of larvae observed in preburn, burn, and postburn years within the macroplots demonstrated that fire was lethal for egg masses laid immediately before the burn and larvae did not move into the burned area (Table 1). Complete mortality of eggs and larvae from prescribed burning has been alluded to in other studies (Siemann et al. 1997, Swengel 1998, Panzer & Schwartz 2001) and demonstrated directly in gall forming wasps (Fay & Samenus 1993) and a Lyceanid butterfly (Schultz & Crone 1998). The mortality of immature life stages inspires criticism for the effects of prescribed fire on rare Lepidoptera while managing for plant communities (Pyle 1997, Schlicht & Orwig 1999). In cases where entire prairie fragments are burned, the high mortality of immature life stages may indeed be a cause for concern, as high immature mortality rates may result in population bottlenecks. Increasingly smaller population sizes in butterfly populations have been linked to an increase in the risk of population extinction (Nieminen et al. 2001). However, when land parcel subdivisions are not frequently burned, lepidopteran populations may be less likely to experience a catastrophic loss of individuals affecting the overall population fitness.

This study suggests that prescribed burning has the potential to limit or encourage the *H. eglanderina* population depending on the size of the burn, the presence of a colonizing population, and burn frequency. Unfortunately, I was unable to measure survivorship and vigor of larvae in the field to determine the effects of the burn on the intrinsic rate of population growth, and this information is essential to determining if the maternal bias for burned plants has an adaptive value to the population. Without survivorship estimates, it can not be known if a burn area acts as a population source or sink, and a strong argument for or against prescribed burning cannot be given. Schultz

and Crone (1998) recommended burning for a Willamette Valley upland prairie endemic butterfly, *Icaricia icarioides fenderi* Macy. They proposed that a rotation of small scale prescribed burns within the butterfly's habitat could maximize the growth rate of the butterfly population while still managing for invasive plant species and the native plant community. Less destructive methods of managing grasslands, such as mowing, may also be a viable management practice combined with rotations of smaller burns, as *H. eglanderina* egg masses were observed to survive a fall mowing event (pers. obs.).

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#### LITERATURE CITED

- AGEE, J. K. 1993. Fire ecology of pacific northwest forests. Island Press, Washington D.C., USA. 493 pp.
- BENZIE, J. A. H. 1986. The distribution, abundance, and the effects of fire on mound building termites (*Trinervitermes* and *Cubitermes* spp., Isoptera: Termitidae) in northern Guinea savanna, West Africa. *Oecologia* 70:559–567.
- BERTWELL, R. L. & H. D. BLOCKER. 1975. Curculionidae from differently managed tallgrass prairie near Manhattan, Kansas. *J. Kansas Entomol. Soc.* 48:319–326.
- BLANCHE, K. R., A. N. ANDERSEN & J. A. LUDWIG. 2001. Rainfall contingent detection of fire impacts: responses of beetles to experimental fire regimes. *Ecol. Appl.* 11:86–96.
- BOYD, R. 1986. Strategies of Indian burning in the Willamette Valley. *Can. J. Anthropol.* 5:65–85.
- CRAWFORD, C. S. & R. F. HARWOOD. 1964. Bionomics and control of insects affecting Washington grass seed fields. Technical Bulletin of the Agricultural Experimental Station, Washington State 44:1–25.
- EVANS, E. W. 1984. Fire as a natural disturbance to grasshopper assemblages of tallgrass prairie. *Oikos* 43:9–16.
- FAY, P. H. & R. J. SAMENUS, JR. 1993. Gall wasp (Hymenoptera: Cynipidae) mortality in a spring tallgrass prairie fire. *Environ. Entomol.* 22:1333–1337.
- FERGUSON, D. C. 1971. The moths of America north of Mexico: fascicle 20.2A Bombycoidea, Saturniidae (part). E. W. Classey and R. B. D. Publications Inc. 153 pp.
- FLEISHMAN, E. 2000. Monitoring the response of butterfly communities to prescribed fire. *Environ. Management* 26:685–695.
- HUEBSCHMAN, J. J. & T. B. BRAGG. 2000. Response of regal fritillary (*Speyeria idalia* Drury) to spring burning in an eastern Nebraska tallgrass prairie, USA. *Nat. Areas J.* 20:386–388.
- LEACH, M. K. & T. J. GIVNISH. 1996. Ecological determinants of species loss in remnant prairies. *Science* 273:1555–1558.
- MCCULLOUGH, D. G. & H. M. KULMAN. 1991. Differences in foliage quality of young jack pine (*Pinus banksiana* Lamb) on burned and clearcut sites: effects on jack pine budworm (*Choristoneura pinus pinus* Freeman). *Oecologia* 87:135–145.
- MORRIS, M. G. 1975. Preliminary observations on the effects of burning on the Hemiptera (Heteroptera and Auchenorrhyncha) of limestone grassland. *Biol. Cons.* 7:311–319.
- NCSS. 2000. Number cruncher statistical software. Kaysville, Utah.

- NIEMENEN, M., M. C. SINGER, W. FORTELIUS, K. SCHÖPS & I. HANSKI. 2001. Experimental confirmation that inbreeding depression increases extinction risk in butterfly populations. *Amer. Nat.* 157:237–244.
- NOSS, R. F., E. T. LAROE, & J. M. SCOTT. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. National Biological Service, Biological Report 28, Washington, D.C.
- OREGON NATURAL HERITAGE PROGRAM. 2001. Rare, threatened, and endangered plants and animals of Oregon. Oregon Natural Heritage Program, Portland, Oregon. 94 pp.
- PANZER, R. 1988. Managing prairie remnants for insect conservation. *Nat. Areas J.* 8:83–90.
- PANZER, R. & M. SCHWARTZ. 2000. Effects of management burning on prairie insect species richness within a system of small, highly fragmented reserves. *Biol. Cons.* 96:363–369.
- PENDERGRASS, K. L. 1995. Vegetation composition and response to fire of native Willamette valley wetland prairies. M.Sc. Thesis, Oregon State University, Corvallis, Oregon. 241 pp.
- PENDERGRASS, K. L., P. M. MILLER & J. B. KAUFFMAN. 1998a. Prescribed fire and the response of woody species in Willamette Valley wetland prairies. *Restoration Ecol.* 6:303–311.
- PENDERGRASS, K. L., P. M. MILLER, J. B. KAUFFMAN & T. N. KAYE. 1998b. The role of prescribed burning in maintenance of an endangered plant species, *Lomatium bradshawii*. *Ecol. Appl.* 9:1420–1429.
- PYLE, R. M. 1997. Burning bridges. *Wings* 20:22–23.
- SCHLICT, D. W. & T. T. ORWIG. 1992. The last of the Iowa skippers. *Amer. Butterflies* 7:4–13.
- SCHULTZ, C. B. & E. E. CRONE. 1998. Burning prairie to restore butterfly habitat: a modeling approach to management tradeoffs for the Fender's blue. *Restoration Ecol.* 6:244–252.
- SIEMANN, E., J. HAARSTAD & D. TILMAN. 1997. Short-term and long-term effects of burning on oak savanna arthropods. *Amer. Midland Nat.* 137:349–361.
- STEIN, S. J., P. W. PRICE, W. G. ABRAHAMSON & C. F. SACCHI. 1992. The effect of fire on stimulating willow regrowth and subsequent attack by grasshoppers and elk. *Oikos* 65:190–196.
- SWENGEL, A. B. 1996. Effects of fire and hay management on abundance of prairie butterflies. *Biol. Cons.* 76:73–85.
- . 1998. Effects of management on butterfly abundance in tallgrass prairie and pine barrens. *Biol. Cons.* 83:77–89.
- TAYLOR, T. H. 1999. Long-term vegetation response to fire of Willamette Valley wet prairie species. M.Sc. Thesis, University of Oregon.
- VOGL, R. J. 1974. Effect of fire on grasslands, pp. 139–194. In Kozlowski, T. T. and C. E. Ahlgren (ed.), *Fire and ecosystems*. Academic Press, New York.

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