Ecology of a Fire-Dependent Moth, *Schinia masoni,* and its Host Plant in Colorado

Bruce A. Byers,[#] Laurie S. Huckaby,[§] and Merrill R. Kaufmann[§]

[#] To whom correspondence should be addressed; 405 Timber Lane
Falls Church, VA 22046 USA Tel: (703) 534-4436Email: bruce.byers@verizon.net

[§] U.S. Forest Service, Rocky Mountain Research Station
240 West Prospect
Fort Collins, CO 80526

Running head: Ecology of the Colorado Firemoth

ABSTRACT

Schinia masoni is a generally rare noctuid moth, endemic to the northern Front Range of Colorado. Its larvae feed on the developing seeds of its host plant *Gaillardia aristata,* blanketflower. The objectives of this study were to investigate the possible fire-dependence of *G. aristata*, and to quantify the relationship between time since a fire and the abundance of *G. aristata* and *S. masoni.* The abundance of blanketflower and *S. masoni* larvae were recorded in four burned areas and in adjacent unburned areas in 2002, and at six additional sites in 2003, representing a range of one to approximately 100 years since a fire. Blanketflower populations increase dramatically at most sites within one year after a fire. *Schinia masoni* can be common in dense, post-fire blanketflower populations. Blanketflower abundance declines over time, and this species becomes uncommon in areas that have not burned in decades. *Schinia masoni* may persist as a fire-dependent metapopulation, colonizing newly-burned "islands" with abundant blanketflowers, and becoming locally extinct where its host plant has declined to low levels in unburned forests. Because of its probable ecological dependence on fire, and a geographic range limited to the northern Colorado, *S. masoni* could appropriately be called the "Colorado firemoth." Its characteristics could make it a sensitive indicator of landscape-scale heterogeneity caused by fires.

Key words: *Schinia masoni*, Colorado firemoth, *Gaillardia aristata*, blanketflower, fire ecology, indicator species, forest restoration

Schinia masoni is a noctuid moth of the subfamily Heliothinae. Like other flowermoths of the genus *Schinia,* its larvae feed on the developing seeds of its host plant, in this case *Gaillardia aristata* Pursh (Asteraceae), commonly called blanketflower (Byers 1989). The burgundy forewings and yellow head and thorax of adult *S. masoni* make them extremely well camouflaged when feeding or resting on the blossoms of *G. aristata* (Fig. 1). *Schinia masoni* is completely dependent on *G. aristata,* its sole host plant, and this relationship must be the result of a long process of coevolution.

In Colorado, *Gaillardia aristata* is found from the grassland-forest ecotone at the edge of the foothills of the Front Range, at elevations of around 1800 meters, to the upper limits of the range of ponderosa pine, in the "mixed conifer" montane forest zone, at elevations of approximately 2700 meters. *G. aristata* can be found blooming from about mid-June to late August, with the blooming period beginning and ending earlier at lower elevations. At a given location blossoms can be present for 4-5 weeks, and a single blossom requires about 2-1/2 weeks to progress from a bud to the dry seedhead stage (Byers 1989).

The life history of *S. masoni* was described by Byers (1989) based on field and laboratory studies. Female *S. masoni* insert eggs between the disk-flowers of *G. aristata*. There are five larval instars, and from hatching to pupation takes approximately 20 days. Because larvae eat blanketflower seeds and detach the ray-flowers at their bases, they cause characteristic ridges on the disk-flower that make their presence easy to detect even without probing into the disk-flower. Pupation takes place in the soil, and pupae probably wait one year before emerging as adults during the next blooming period of their host plant.

Schinia masoni is endemic to the northern Front Range of Colorado, found approximately from the Platte-Arkansas Divide northward to the Wyoming border. In Colorado it has been reported from El Paso, Douglas, Jefferson, Boulder, and Larimer counties, and a few specimens have been reported from the southernmost part of Albany Co., Wyoming (C. Harp, pers. comm.). Its range is only a small part of the range of its host plant *Gaillardia aristata*, which occurs northward from Colorado into Canada and westward to Washington, Oregon, and British Columbia (Biddulph 1944). *Schinia masoni* is an atypical flowermoth in this regard; the distribution of most flowermoth species overlaps most of the range of their host plant or plants (C. Harp, pers. comm).

Schinia masoni is generally rare. It is not unusual to see only a few adults when searching thousands of blossoms of *G. aristata* at the peak of the blooming period. Fewer than 100 specimens exist in museum collections (Byers 1989; C. Harp, pers. comm.).

Personal observations by the first author in 1992 indicated that in the area burned by the 1989 Black Tiger Fire, west of Boulder, blanketflowers were abundant and moths were relatively common, in contrast to the scarcity of flowers and rarity of moths in nearby unburned areas. The objectives of the study reported here were to investigate this apparent fire dependence of blanketflower, and to quantify the relationship between time since a fire and the abundance of *G. aristata* and *S. masoni.* A longer-term goal of this research is to determine whether *S. masoni* might serve as an indicator species for understanding and monitoring the fire-related heterogeneity of forest landscapes in the Colorado Front Range, and therefore be of interest to forest managers involved in ecological restoration or fire hazard reduction activities.

Figure 1. *Schinia masoni* on *Gaillardia aristata*

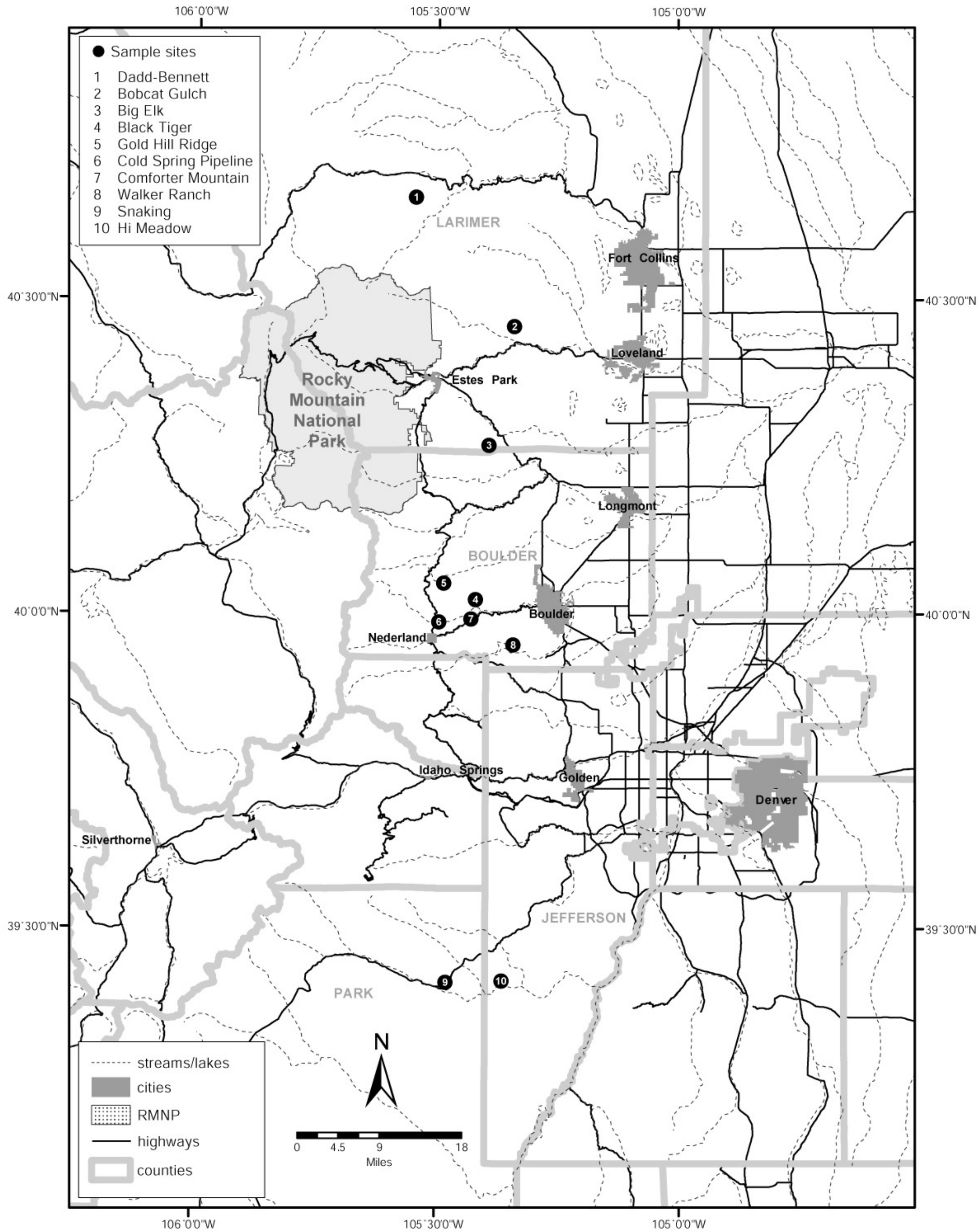
METHODS

Locations of more than 30 past fires in the Colorado Front Range were identified from records of the Pike and Arapaho-Roosevelt National Forests and from personal communication with knowledgeable individuals. Some of these were wildfires and some were prescribed fires. Ten burned areas were visited in 2002, and four were selected as study sites based on the presence of blanketflower, *Gaillardia aristata*. Five additional burn sites and one mechanically disturbed site with blanketflowers were added as study sites in 2003 (Table 1). The ten study sites range from approximately 2,200 to 2,700 meters in elevation. The most recent fires at these sites occurred from one to an estimated 98 years ago. Their locations are shown on the map in Figure 2. Soils at these sites were derived either from granitic or metamorphic rocks (GTR Mapping 2003), and were often course and dry, especially on granitic substrates.

Table 1. Study Sites

Name	Elevation (m)	Date of Fire or Disturbance	Type of Fire or Disturbance	Year Data Collected
Big Elk	2195	2002	wildfire	2003
Black Tiger	2652	1989	wildfire	2002, 2003
Bobcat Gulch	2256	2000	wildfire	2002, 2003
Cold Spring Pipeline	2500	1999	mechanical	2003
Comforter Mountain	2439	1976	wildfire	2003
Dadd-Bennett	2470	2001	prescribed	2002, 2003
Gold Hill Ridge	2713	1905	wildfire	2003
Hi Meadow	2226	2000	wildfire	2003
Snaking	2500	2002	wildfire	2003
Walker Ranch	2195	2000	wildfire	2002, 2003

Figure 2. Map of study sites.



Each burn site was surveyed for the presence of *G. aristata*, and also for adults or larvae of *Schinia masoni*. A 100-meter long transect was laid out at each study location and its position and elevation recorded with a handheld GPS unit. Locations of all transects were plotted on 1:24,000 topographic maps. . Photographs were taken along each transect to provide visual documentation. Photographs from 2002 were used to align the 2003 transects in the same locations where possible.

The number of *G. aristata* blossoms was recorded meter by meter along each transect, within a distance of three meters on each side of the tape. Blossoms in any stage of blooming, from bud to seedhead stage, were counted in each of these 1 m by 3 m segments of the transect. The number of blossoms containing larvae of *S. masoni* was also recorded within each 3 m sq. segment of the transect. Blossoms containing larvae are easily identified by the characteristic damage that larvae produce on the disk-flower. Each blossom was carefully inspected for suspicious damage to the disk-flower, and disk-flowers were gently pulled apart to visually confirm the presence of suspected larvae.

In 2002, abundance data also were collected on transects in unburned areas within one kilometer or less of the Black Tiger, Dadd-Bennett, and Walker Ranch burned sites. Care was taken to select a location for an unburned transect that was as equivalent as possible in slope, aspect, tree density, and species composition to the corresponding transect in the burned area. In the burned areas at each of these sites, between 50 and 100% of the trees had been killed by the fire. At the Bobcat Gulch site no equivalent site that was completely unburned could be found within one kilometer, so a reference transect was set in an area that had been only very lightly-burned. In the lightly-burned area no trees had been killed by the fire, even saplings one meter tall, so we reasoned that the fire must have burned there as a low intensity surface fire.

The same transects at these four sites were resurveyed in 2003 using the same methods. The blooming period of *G. aristata* was somewhat delayed in 2003 compared to 2002, and the sites were not always visited on the same date as the previous year. Rather, they were visited at approximately the same stage in the blooming cycle. Data were collected between 12-23 July, 2002, and between 15-24 July, 2003.

Statistical analysis of these abundance data is complicated because only one transect was sampled at each study site. The distribution of counts of blossoms and larvae along transects were compared to Poisson, negative binomial, and Neyman Type A distributions, but none were found to adequately describe the clumpiness of observed counts. Chi-squared row-by-column contingency tables were considered, but these are also biased by the lack of independence of the cell counts along the transects. Interpretations of the abundance data are therefore based on comparisons of presence or absence, and relative abundance, of blossoms and larvae among sites and years.

Cross-dated stand age and fire scar samples from increment cores were used to reconstruct the fire history of the Gold Hill Ridge study site, a mountain meadow in which *G. aristata* were relatively abundant and *S. masoni* were present. This was the only study site at which the date of the last fire was not known from historical records. Standard dendrochronological methods were used (Stokes and Smiley 1968).

We conducted a germination study of *G. aristata* using seeds collected in August 2003 at Dadd-Bennett, Cold Spring Pipeline, and Gold Hill Ridge in October and November 2003. To break the physiological dormancy of these seeds and enable germination without a long, overwinter dormant period, a cold-moist stratification technique was used (Wick et al. 2001). The purpose of this study was to determine whether charred wood and ash stimulates germination in *G. aristata,* as it has been shown to do in some fire-following herbs from in California chaparral (Keeley and Pizzorno 1986). Charred wood and ash was obtained by burning twigs, small branches, cones, and needles of mixed ponderosa pine and Douglas fir to simulate the results of a fire in Front Range ponderosa pine and mixed conifer zones. This charred mixture was ground with a mortar and pestle, and 150 g was added to 2 liters of tap water to produce ash "tea."

Approximately 350 seeds from three study sites were divided into two treatment groups, and placed in smaller samples of up to 20 seeds on folded unbleached paper towels. Seeds from different sites were kept separate, half from each site in each treatment group. These were moistened with either plain tap water or ash tea, sprayed from spray bottles. For the ash-treatment group, approximately 2 g of finely powdered charcoal and ash were also sprinkled on the towels around the seeds. The moistened towels were folded in half over the seeds and placed in plastic bags. The samples were kept in the dark at 4 degrees C for 28 days. At the end of the cold moist stratification period, seeds were examined for germination. Samples that had been stratified together were placed on filter paper in a 10 cm diameter petri dish. Powdered charcoal was again sprinkled on the ash-treatment samples, and these were moistened with ash tea. The control samples were moistened as before with plain tap water. All samples were then covered and placed in a growth chamber maintained on a 12 hour light–12 hour dark cycle at 19 degrees C. They were checked each day for germination and re-moistened if needed with either plain water or ash tea, for nine days, after which time no further germination occurred.

RESULTS

At all study sites except Gold Hill Ridge, the date of the last fire was known from historical records. Reconstruction of the fire history of the Gold Hill Ridge study site from tree cores and fire scars showed a complex disturbance history. This site is a meadow that is being invaded by aspen and ponderosa pine. The invasion by aspen, through resprouting of a cohort of ramets from underground roots, began in the 1940s. A cohort of ponderosa pine appears to have started growing in the mid-1960s. There is nothing in the fire scar record to indicate that these pulses of regeneration followed a fire, although it is possible that a fire at one or both of those times occurred but scarred no trees. The most recent major fire seems to have been during the dormant season between 1905 and 1906, which scarred four large live ponderosa pines at the edge of the meadow.

Blanketflowers become very abundant in burned areas in the years following fires compared to control areas (Table 2). In areas not recently burned, this plant is a negligible component of the understory community, if not entirely absent.

Blanketflowers can be very common in recently burned areas, with densities up to approximately three blossoms per square meter only two years after a fire (Table 3). Even one year after a fire there is clear evidence that populations of *G. aristata* are stimulated by burning. Populations of blanketflowers typically have a patchy distribution within burns. Abundance varies greatly among sites.

Abundance of *Schinia masoni* also varies greatly among sites (Table 3). Where they are present, moths can be quite common. However, moths are not present at all sites, even those with very dense populations of blanketflowers. Moth populations appear to persist at some sites even though populations of their host plant decline dramatically compared to their abundance in the first few years after a fire. The highest percentage of blossoms with moth larvae at any site was at the 14-year-old Black Tiger burn, where nearly 24% of blossoms had larvae.

The Cold Spring Pipeline site shows that mechanical disturbance of soil, like fire, may result in a dramatic increase in the population of blanketflowers compared to undisturbed areas.

Compounds in charcoal and ash do not appear to stimulate germination in *G. aristata.* No statistically significant differences in germination between ash-treated seeds and controls were observed either at the end of a cold and moist stratification period or after nine days in a growth chamber.

Table 2. Blanketflower Abundance in Burned and Unburned Areas (# of blossoms/600 m. sq)

Site (and years since fire)	Burned Area	Unburned Area
Black Tiger (13 years)	73	2
Bobcat Gulch (2 years)	1,916	127 (lightly burned)
Dadd-Bennett (1 year)	687	0
Walker Ranch (2 years)	626	0

Table 3: Blanketflower and Firemoth Abundance

Site	Time Since Fire	Blanketflower Abundance (blossoms/600 m2)	Moth Abundance (larvae/600 m2)
Big Elk	1 year (in 2003)	171	0
Black Tiger	13 years (in 2002)	73	16
	14 years (in 2003)	96	23
Bobcat Gulch	2 years (in 2002)	1,916	316
	3 years (in 2003)	938	82
Cold Spring Pipeline	4 years (in 2003) (since mech. disturb.)	260	58
Comforter Mountain	27 years (in 2003)	226	13
Dadd-Bennett	1 year (in 2002)	687	0
	2 years (in 2003)	1,254	0
Gold Hill Ridge	~ 98 years (in 2003)	342	8
Hi Meadow	2 years (in 2003)	307	0
Snaking	1 year (in 2003)	125	0
Walker Ranch	2 years (in 2002)	626	57
	3 years (in 2003)	601	51

Table 4. Seed Germination

Time	**Treatment**		
	Water Only	**Ash + Water**	
28-days cold/moist stratification	**9/172 (5.2%)**	**16/171 (9.4%)**	Fisher's exact test statistic = 2.12, p = 0.15, N.S.
+ 9-days warm/light-dark germination	**130/172 (75.6%)**	**121/171 (70.8%)**	Fisher's exact test statistic = 1.01, p = 0.33, N.S.

DISCUSSION

Stimulation of *Gaillardia aristata* by Fire

The dramatic stimulation of *Gaillardia aristata* following fire is demonstrated by the data from the four study sites in 2002 and reinforced by data collected from additional sites in 2003. Blanketflower is clearly an early-successional species that colonizes burned areas. Data from the severely burned and lightly burned transects sampled in the Bobcat Gulch burn in 2002 suggest that *Gaillardia aristata* is more common following hot, stand-replacing fires than after cooler surface fires.

Its rapid colonization of burned areas suggests that blanketflower is a "residual colonizer" (Arno and Allison-Bunnell 2002), whose seeds sprout from a soil seed bank in which they have remained dormant, for many decades perhaps, until stimulated to germinate by the conditions following a fire (Archibold 1989). It is also possible, but much less likely, that seeds are dispersed in very large numbers over very long distances into burned areas within one year by an as yet unknown mechanism or agent of dispersal. The structure of *G. aristata* seeds does not resemble that of typical wind-dispersed species, nor do they appear to have characteristics suitable for dispersal by birds or mammals. Evidence from other fire-adapted communities shows that seeds of some species not found in the aboveground community can be found in the soil seed bank. For example, in a ponderosa pine community in eastern Washington seeds of more than 20 species not present aboveground were found in the soil (Pratt et al. 1984), and 19 such species were found in wiregrass flatwoods in Florida (Maliakal and Menges 2000).

Data from unburned transects collected in 2002 show that *G. aristata* virtually disappears as a component of the understory vegetation in long-unburned ponderosa pine and mixed conifer forests. However, it may persist at reasonable densities in mountain meadows for decades after a fire, such as at the Black Tiger, Comforter Mountain, and Gold Hill Ridge study sites.

The data show that the abundance of *G. aristata* can vary greatly between sites of the same age since fire. Soil type may be a factor in this variability. Blanketflower appears to be less common on coarse, dry, granitic soils in the Pikes Peak area than on soils derived from metamorphic rocks farther north, but further research is needed to understand the cause of this apparent pattern.

Serendipitous observations made in 2002 showed that mechanical disturbance of the soil also creates the conditions needed to stimulate *G. aristata* germination. At the site of pipeline construction along Cold Spring Road north of Nederland in Boulder County, *G. aristata* were abundant along the edges of the pipeline cut. This reinforces the conclusion that *G. aristata* is a disturbance-dependent, early successional plant, which requires disturbance to eliminate competitors or change the conditions for germination of its seeds. Soil disturbance by pocket gophers, *Thomomys talpoides,* in montane meadows may stimulate germination of *G. aristata* seeds and facilitate persistence of blanketflower populations at these sites.

Fire-created compounds found in charcoal and ash do not appear to stimulate germination in *G. aristata* as they have been shown to do in some herbaceous species found in California chaparral ecosystems (Keeley and Pizzorno 1986). The fact that mechanical disturbance also stimulates germination of blanketflower suggests that it is biological or physical conditions created by fire, rather than chemical cues, that are responsible. Increased soil temperatures and light availability caused by removal of the tree canopy, surface vegetation, duff layer, and the exposure of mineral soil, could be a possible explanation. Decreased competition with other plants could also play a role.

Colonization of Blanketflowers by *Schinia masoni*

Moths colonize some, but not all, populations of blanketflowers in burns within two years following a fire. They were present, and even relatively common, at Bobcat Gulch and Walker Ranch two years after fires, but absent at Dadd-Bennett and Hi Meadow after the same length of time. Moths had not colonized blanketflower populations at Big Elk, Dadd-Bennett, or Snaking burn sites one year after those fires. At Bobcat Gulch and Walker Ranch, the abundance of moths in the second year following fires suggests that moths colonized those burns after one year, enabling relatively large populations to develop by the second year.

Gaillardia aristata and *S. masoni* can persist for decades following a fire, as seen at the Black Tiger, Comforter Mountain, and Gold Hill Ridge study sites. Dispersers from such residual, core populations may opportunistically colonize the dense blanketflower populations that develop in nearby burns. Because *G. aristata* virtually disappears from the understory community in unburned ponderosa pine or ponderosa pine-Douglas-fir forests, moths must eventually disperse and colonize new burned areas to persist within the landscape. Like many species that live in early-successional communities, these moths probably exist as a metapopulation – that is, a "shifting mosaic of temporary populations linked by some degree of migration" (Primack 2000). Concepts and methods of island biogeography and metapopulation theory should be applicable to an understanding of the metapopulation dynamics of *S. masoni* as it colonizes newly-burned "islands" where dense blanketflower populations can develop, and as it becomes locally extinct on other such "islands" where blanketflower populations have declined to very low levels (Hanski and Simberloff 1997; Hanski and Singer 2001; Krauss et al. 2003).

Moth larvae are significant seed predators. Up to 24% of blossoms may have larvae (as at Black Tiger in 2003), and one larva may eat the seeds of several blossoms (Byers 1989). This ecological relationship could mean that *S. masoni* populations suppress the reproduction of *G. aristata,* their sole host plant -- which appears to be a short-lived (2-3 year) perennial – and thereby become food-limited. Moths may be partly responsible for the decline in *G. aristata* populations over time following a fire.

Schinia masoni as an Indicator Species

Like most flowermoths, *Schinia masoni* has no common name. It has evolved a complete dependence on a single, disturbance-dependent host plant. Because of this ecological and evolutionary dependence on fire, the most ecologically important natural disturbance in the Front Range, and because its limited range is restricted almost entirely to Colorado, it could appropriately be called the "Colorado firemoth."

This study suggests that *Schinia masoni* may persist within its limited range as a metapopulation, dependent on the size and frequency of fires that result in dense populations of its host plant, *Gaillardia aristata*. Its presence and abundance at a site should be related to the fire-created heterogeneity of the surrounding landscape, and so this species may prove to be a sensitive indicator of such heterogeneity. If so, monitoring populations of *Schinia masoni* may be of interest to forest managers attempting to restore a more ecologically natural forest landscape. Butterflies have been proposed as indicators of restoration progress in southwestern ponderosa pine forests (Minard 2003; Waltz and Covington 1999).

A fundamental understanding of the historical fire regime for ponderosa pine and mixed conifer forests in the Front Range is required in order to place hypotheses about the population dynamics of *S. masoni* into proper context. Studies in several areas have attempted to elucidate the historical fire regime. The findings are complex, and suggest that elevation, topography, climatic variation, human activities, and perhaps soil characteristics all can influence fire interval, severity, and spatial extent in ways that are probably area-specific (Brown et al. 1999; Veblen 2003; Veblen et al. 2000).

In the area around Cheesman Lake, a reservoir on the South Platte River in the southern Front Range, the mean fire interval ranged from about 10 years to about 60 years (Brown et al.1999; Kaufmann, Huckaby, and Gleason 2000; Kaufmann, Regan, and Brown 2000). This area experienced a mixed-severity fire regime, with both surface fires and widespread stand-replacing fires. Historical fires ranged in size from small patches of trees to at least 4000 hectares, covering the entire study area. The mean fire interval for widespread fires at the Cheesman site was 59 years. In contrast to the historical landscape at Cheesman, the present forest landscape in adjacent areas where logging and fire suppression occurred has few openings or low-density forest, a much higher tree density, and a much higher proportion of Douglas-fir mixed with ponderosa pine.

Work by Veblen and colleagues in the northern Front Range provides another sample of the historical fire regime (Veblen et al. 2000). Mean fire intervals for widespread fires ranged from about 10 years at low elevations to more than 30 years at higher elevations. Fires were generally less severe at low elevations with a shorter fire-return interval. At higher elevations, the data suggest a mixed-severity fire regime, which included surface fires but in which stand-replacing fires were common. In some years fires affected large portions of the landscape, as indicated by the fact that many widely dispersed sites recorded fires in the same years. All elevation zones showed a decline in fire frequency after about 1920 that is especially marked for years of widespread fires. This is undoubtedly at least partly the result of the adoption of a fire exclusion policy by the U.S. Forest Service in 1910 (Arno and Allison-Bunnell 2002), as well as the result of previous logging, grazing, and earlier widespread fires (Veblen et al. 2000).

A recent study of mixed conifer forests at elevations between 7500 and 9000 feet in Larimer County, even farther north in the Front Range, suggests that they also experienced a mixed-severity fire regime (Huckaby unpublished data). This is indicated by even-aged patches of lodgepole pine and aspen, interspersed with much more open stands dominated by ponderosa pine, and meadows which appear to have been permanent, not necessarily fire-maintained.

Fire suppression in the Colorado Front Range generally seems to have led to increased tree densities and invasions of trees into meadows and grasslands at forest-grassland boundaries (Mast et al. 1998). In the historical forest landscapes of the Front Range the total area of forest patches burned with moderate to high severity – stand-replacing or nearly stand-replacing fires – appears to have been much larger than during the 20th century. That means that such patches must have been much closer together than now.

In such a landscape, *S. masoni* may have been more abundant than today. From a firemoth's perspective, finding and colonizing a dense, fire-successional blanketflower population may now be more of a challenge than it has been throughout the evolutionary history of this species, because such burned "islands" are fewer and farther between than ever before.

The hypothesis that the presence or abundance of *S. masoni* is related to fire-created landscape heterogeneity suggests an explanation for some of the results reported above. The Dadd-Bennett study site, with a dense population of blanketflowers, but no firemoth colonization within the first two years, appears to be a relatively isolated burn within a relatively homogeneous forest landscape, in which there have been fewer recent burns with large stand-replacing components than in areas farther south. This site is 28.6 km northwest of Bobcat Gulch, a site with a large firemoth population. It appears that *Schinia masoni* has so far been unable to reach the Dadd-Bennett site. In contrast, all study sites in Boulder County (Black Tiger, Cold Springs Pipeline, Comforter Mountain, Gold Hill Ridge, and Walker Ranch) have firemoths, and all are found within about 10 km of each other in a complex, heterogeneous landscape of forest, old burns and ridgetop meadows. Future research will seek to test this hypothesis and clarify the dependence of the Colorado firemoth on a fire-created heterogeneous landscape.

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LITERATURE CITED

Archibold, O.W. 1989. Seed banks and vegetation processes in coniferous forests. Pages 107-122 in M.A. Leck, V.T. Parker, and R.L. Simpson, editors, Ecology of soil seed banks. Academic Press, San Diego, CA.

Arno, S.F., and S. Allison-Bunnell. 2002. Flames in our forest: Disaster or renewal? Island Press, Washington, D.C. 227 pp.

Biddulph, S.F. 1944. A revision of the genus *Gaillardia.* Research Studies of Washington State College 12: 195-256.

Brown, P.M., M.R. Kaufmann, and W.D. Shepperd. 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. Landscape Ecology 14: 513-532.

Byers, B.A. 1989. Biology and immature stages of *Schinia masoni* (Noctuidae). Journal of the Lepidopterists' Society 43: 210-216.

GTR Mapping. 2003. Colorado Geologic Highway Map. P.O. Box 1984, Canyon City, COI 81215.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5-26 in I. Hanski and M.E. Gilpin, editors, Metapopulaion biology: ecology, genetics, and evolution. Academic Press: Sand Diego, CA.

Hanski, I. and M.C. Singer. 2001. Extinction-colonization dynamics and host-plant choice in butterfly metapopulations. American Naturalist 158: 341-353.

Kaufmann, M.R., L.S. Huckaby, and P. Gleason. 2000. Ponderosa pine in the Colorado Front Range: Long historical fire and tree recruitment intervals and a case for landscape heterogeneity. Proceedings, Joint Fire Science Conference and Workshop, Boise, ID, June 1999. Vol 1, pp. 153-160.

Kaufmann, M.R., C.M. Regan, and P.M. Brown. 2000. Heterogeneity in ponderosa pine/Douglas-fir forests: Age and size structure in unlogged and logged landscapes of central Colorado. Canadian Journal of Forest Research 30: 698-711.

Keeley, S.C., and M. Pizzorno. 1986. Charred wood stimulated germination of two fire-following herbs of the California chaparral and the role of hemicellulose. American Journal of Botany 73: 1289-1297.

Krauss, J., I. Steffan-Dewenter, and T. Tscharntke. 2003. Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. Oecologia 137: 591-602.

Maliakal, S.K. and E.S. Menges. 2000. Community composition and regeneration of Lake Wales Ridge wiregrass flatwoods in relation to time-since-fire. Journal of the Torrey Botanical Society 127: 125-138.

Mast, J.N., T.T. Veblen, and Y.B. Linhart. 1998. Disturbance and climatic influences on age structure of ponderosa pine at the pine/grassland ecotone, Colorado Front Range. Journal of Biogeography 25: 743-767.

Minard, A. 2003. Butterflies as indicators of restoration progress. Working Papers in Southwestern Ponderosa Pine Forest Restoration. Ecological Restoration Institute, Northern Arizona University, Flagstaff, AZ.

Pratt, D.W., R. Alan Black, and B.A. Zamora. 1984. Buried viable seed in a ponderosa pine community. Canadian Journal of Botany 62: 44-52.

Primack, R.B. 2000. A Primer of Conservation Biology, 2nd Edition. Sinauer Associates, Inc.: Sunderland, Mass. 319 pp.

Stokes, M.A., and T.L. Smiley. 1968. An Introduction to tree-ring dating. University of Chicago Press, Chicago. 68 pp.

Veblen, T.T. 2003. Historic range of variability of mountain forest ecosystems: concepts and applications. The Forestry Chronicle 79: 223-226.

Veblen, T.T., T. Kitzberger, and J. Donnegan. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. Ecological Applications 10: 1178-1195.

Waltz, A.E.M., and W.W. Covington. 1999. Butterfly richness and abundance increase in restored ponderosa pine ecosystem (Arizona). Ecological Restoration 17: 244-246.

Wick, D., T. Luna, J.Evans, and J. Hosokawa. 2001. Propagation protocol for production of container *Gaillardia aristata* Pursh. plants (160 ml containers); Glacier National Park, West Glacier, Montana. *in* Native Plant Network. URL: http://www.nativeplantnetwork.org (accessed 22 January 2004). Moscow (ID): University of Idaho, College of Natural Resources, Forest Research Nursery.