LAND MANAGEMENT IMPLICATIONS FOR *HEMILEUCA MAIA* (LEPIDOPTERA: SATURNIIDAE) HABITAT AT MANUEL F. CORRELLUS STATE FOREST, MARTHA'S VINEYARD, MASSACHUSETTS

A Thesis Presented

by

SARAH A. HAGGERTY

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Approved as to style and content by:

Paul R. Sievert, Chair

Paul Z. Goldstein, Member

Michael W. Nelson, Member

William A. Patterson III, Member

Matthew J. Kelty, Department Head
Department of Natural Resources Conservation

DEDICATION

To Mickey Callahan: for his tireless work, his kindness, his wit, his culinary expertise, and his support. Mickey took us under his wing, looked after us, listened to us, started early, worked hard, told us stories, heard our complaints, and made us laugh. I am honored to have known him for these short three years, and will sorely miss him now that he is gone.

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CHAPTER 1

INTRODUCTION

Early seral habitats in the northeastern U.S. are being threatened by succession brought on by the alteration of natural ecosystem dynamics (Noss 1995). In fire-dependent systems such as sandplain barrens, this is compounded by the threat of catastrophic fire from increased fuel loads created by long-term fire suppression. Efforts are currently underway in many areas to restore open habitats through the reintroduction of natural disturbances or by alternative techniques which mimic their effects. In fire prone systems, the goal of these efforts is twofold: 1) to reduce fire danger in areas with heavy fuel loads and 2) to restore natural open habitats. The effects of such management on the native insect species, including rare species dependent on open systems, are just beginning to be examined (Swengel 2001, Swengel and Swengel 2001, Panzer and Schwartz 2002).

Phytophagous insect species are sensitive to habitat alterations which can affect their survival rate. Survival of Lepidoptera is tied closely to the feeding success of the larval stage, which is controlled by the nutrients available in host plants, the ability to reach and maintain ideal feeding temperatures, and the avoidance of predators and parasitoids (Stamp 1993, Tuskes et al. 1996, Young 1997). Land management affects these criteria directly (e.g. through the removal or increased production of host plants) and indirectly (e.g. by altering vegetation structure which in turn can affect predator hunting success).

Manuel F. Correllus State Forest (MFCSF) on Martha’s Vineyard, MA is located on a sandplain—an outwash plain with glacially-derived, nutrient-poor, sandy soils. Such areas support unique, globally rare plant communities which in turn support a number of rare insect species. The pitch pine, oak, and scrub oak dominated communities of MFCSF are home to over 20 insect species considered rare in Massachusetts, and many more that are regionally rare. Many of these species require open shrubby or grassy habitats, which have been reduced in recent decades through the removal of fire as a disturbance agent. This reduction in insect habitat is coupled with an increase in fire danger with heavier fuel loads. Previous efforts to reduce fire danger on MFCSF have depended on the creation of fire breaks throughout the Forest, using a plowing technique to transition the native shrub communities into manmade grasslands (Foster and Motzkin 1999). Alternatives which can reduce fire danger but retain the native vegetation, and thus the habitats of rare insect species on MFCSF, are examined in this study. The habitat needs of one species of Special Concern, *Hemileuca maia* (Drury) (Saturniidae), and the effects of fuel reduction techniques (thinning of pitch pine, mowing of shrubs, grazing of shrubs and herbs, and burning) on that habitat are examined.

Hemileuca maia is at the northern edge of its range on Martha's Vineyard, where it feeds almost exclusively on scrub oak (*Quercus ilicifolia* and *Q. prinoides*), while in the southern portion of its range it feeds on a variety of tree oak species (Tuskes et al. 1996, Martinat et al. 1997). Host plant choice is examined in this study, comparing *H. maia* growth rates and pupal weights resulting from feeding on leaves of tree oak and scrub oak species, as well as on previously disturbed and undisturbed *Q. ilicifolia* plants. A distinction between previously disturbed *Q. ilicifolia* and undisturbed *Q. ilicifolia* was made to evaluate potential effects of management, such as the techniques used to reduce fire danger, on *H. maia*. The unique pressures individual populations of a species face can determine their success and very survival, and understanding what drives host plant and habitat selection can aid land managers in their attempts to conserve rare insect species.

CHAPTER 2

IMPLICATIONS OF FIREBREAK EXPANSION ON *HEMILEUCA MAIA* (LEPIDOPTERA: SATURNIIDAE) HABITAT

Introduction

Fire-dependent systems, such as those found on sandplains where soils are dry and nutrient poor, are currently threatened by succession where fire suppression has been a large part of the management philosophy (Habeck 1992, Finton 1998, Goldstein 1997, Barbour et al. 1998, Panzer and Schwartz 2000). As trees and dense shrubs invade areas previously dominated by grasses and low sparse shrubs, the local insect communities shift as well. This change in vegetation towards larger dominance by woody plants also leads to an increase in fuel loading and subsequently to an increase in the potential for catastrophic fire.

In the U. S., early successional habitats were historically maintained through a variety of disturbances such as fire, grazing, hurricanes, and salt spray near the coast (Foster et al. 2004, Griffiths and Orians 2004). Europeans also influenced the landscape by mowing, timber cutting and plowing, which kept much of the Northeast in an open state (Foster et al. 2004). With farm abandonment in New England beginning in the 1800s, and increased fire suppression efforts following catastrophic fires on sandplains in the nineteenth and early twentieth centuries, these disturbances were dramatically reduced (Pyne 1984).

Currently, efforts are underway to reduce fuel loads and restore early successional communities using management techniques such as thinning, mowing, grazing, and prescribed fire to mimic historic disturbance patterns (Dunwiddie et al. 1997, Rudnicky et al. 1997, Panzer and Schwartz 2000, Lezberg et al. in press). Effects of these techniques on the insect fauna of sandplains, grasslands, and other open habitats are beginning to be examined as well (Swengel 2001, Swengel and Swengel 2001, Panzer and Schwartz 2002). A recent comprehensive literature review of insect responses to fire and other conservation management techniques, suggests that many variables affect the response of insects to management (Swengel 2001). Type, timing, intensity, and frequency of management, as well as species specific phenology, motility, and protection from heat and desiccation, all influence what effects are seen in the insect populations. Host-plant specificity, as well as availability and proximity of colonizers, affect the rate of reintroduction into recently disturbed areas (Swengel 2001).

One of the largest undeveloped sandplains in Massachusetts exists in the Manuel F. Correllus State Forest (MFCSF) on the island of Martha's Vineyard. Over 2100 hectares of barrens vegetation remain, providing critical habitat for numerous species of conservation concern in Massachusetts. MFCSF has one of the highest known concentrations of terrestrial animals found on the state's list of threatened and endangered species (Goldstein 1997, Foster and Motzkin 1999, MNHESP 2001). Some of these species have been extirpated from mainland New England, and others represent the only New England populations ever recorded (Goldstein submitted). Others may be disjunct populations of prairie species more common to the Midwest (Goldstein 1997, Mehrhoff 1997), as many of them depend on open habitats for survival.

Nearly a century of fire suppression has led to a reduction in the amount of grasslands and open shrublands found at MFCSF, and have left heavy fuel loads of highly flammable trees and shrub thickets on the landscape. Coupled with an increase in private housing development on adjacent lands, MFCSF now offers the potential threat of catastrophic fire, which could threaten lives and property (Foster and Motzkin 1999, Mouw 2002). As an early response to this inherent fire danger, a series of firebreaks was established, beginning in the 1920's, around and throughout what is now MFCSF in an attempt to stop the spread of fires, and to provide access routes for fire suppression personnel (Foster and Motzkin 1999, Mouw 2002). However, a recent study has suggested that the current firebreak width of 15-40 meters may not be sufficient to stop most wildfires (Mouw 2002). Firebreaks were originally created by harrowing—a plowing technique—which causes a shift in native vegetation away from shrub-dominated communities toward man-made grasslands. It is primarily the native shrubland communities that support many of the insect species of conservation concern on the Northeastern sandplains (Wagner et al. 2003). There is thus a need to develop techniques to reduce wildfire hazard at MFCSF, while maintaining the natural plant communities and structure on which many of these rare species depend.

This study examines alternative methods for firebreak expansion and maintenance to assess their effectiveness in providing the physical structure and plant species composition required by rare insect species at MFCSF. Twenty-two such species have been documented on the State Forest. Because many of these species are very rarely encountered, a direct study of the impacts of the various firebreak expansion methods on all species is beyond the scope of this study. One species of moth, *Hemileuca maia*, is locally common and easily sampled in the larval stage at MFCSF and is a species of Special Concern in Massachusetts due to its specialized habitat needs. This species is limited to sandplains in New England where its early instars feed gregariously on scrub oaks (*Quercus ilicifolia* and *Q. prinoides*). Because the study is limited to three years and the treatment plots are small and closely situated allowing for easy movement of moths between plots, the effects of management on the insect population are not examined directly. Instead, this study examines the impacts of alternative firebreak fuel reduction techniques (thinning, mowing, grazing, and prescribed burning) on larval habitat characteristics of *H. maia* within an experimental fuels break area. Larval habitat characteristics were first quantified by sampling plots with and without larvae across the Forest. Several habitat characteristics were measured at each plot in order to describe *H. maia* habitat characteristics for a variety of vegetation or land use types across the Forest. Three characteristics relating to the biological needs of larval *H. maia* were identified as being especially important, and examined in detail to develop a model of *H. maia* preferred habitat. These variables were: 1) canopy cover, 2) scrub oak stem density, and 3) amount of host plant in the area, quantified as an "importance value" relating to the cover/abundance of *Q. ilicifolia*. The effects of fuels management practices on these characteristics were then investigated in the experimental fuels break.

Materials and Methods

Study Site

Martha's Vineyard is an island, approximately 22,000 ha in size, located 8 kilometers southeast of mainland Massachusetts. It has a mild maritime-influenced coastal New England climate with temperatures averaging 0° C in winter and 20° C in summer and an annual precipitation of 120 cm (Foster et al. 2002). Throughout recorded history, the island has seen heavy use by humans; before 1600 A.D. it was home to a population of about 3,500 Native Americans and after 1641 A.D. Europeans manipulated the landscape through settlement and agriculture. During the height of the European colonial era, colonists raised nearly 20,000 head of livestock including 15,000 sheep (Fletcher and Roffinoli 1986, Dunwiddie 1994, Foster and Motzkin 1999). The well-drained sandy soils formed from glacial outwash deposits, coupled with the lack of large bodies of water, left the center of the island dry and virtually uninhabited (Foster and Motzkin 1999). This part of the island is now occupied by a woodland/shrubland that includes over 2000 hectares in MFCSF. Soils are notable for their lack of an extensive Ap (plow) horizon and their poor water holding capacity (Fletcher and Roffinoli 1986, Foster and Motzkin 1999, Mouw 2002). The overstory vegetation is dominated by combinations of tree oak species (*Q. alba, Q. stellata,* and *Q. velutina*) and pitch pine (*Pinus rigida*). The forest also contains plantations of mostly white, red, and Scotch pine (*P. strobus, P. resinosa, P. sylvestris)*, plus white spruce (*Picea glauca*) (Dunwiddie 1994, Foster and Motzkin 1999, Mouw 2002). The shrub layer is dominated by scrub oak (*Q. ilicifolia*), young tree oak (*Quercus* spp.*)* and white pine (*Pinus strobus*), as well as dwarf Chinquapin oak (*Q. prinoides*), black huckleberry (*Gaylussacia baccata*), blueberry species (*Vaccinium* spp.), sweet fern (*Comptonia peregrina*), and sheep laurel (*Kalmia angustifolia*). The herb layer contains a number of species including Pennsylvania sedge (*Carex pennsylvanica*), wintergreen (*Gaultheria procumbens*), pink lady's slipper (*Cypripedium acaule*), mayflower

(*Epigaea repens*), and bracken fern (*Pteridium aquilinum*). The Forest is bounded by a 15 – 40 m wide firebreak, and within the forest is a grid of firelanes at roughly 0.8 km intervals (Foster and Motzkin 1999, Mouw 2002).

Mouw (2002) used aerial photography and relevé sampling (Mueller-Dombois and Ellenberg 2002) to classify the vegetation of MFCSF into seven broad community types for landscape level fire behavior modeling. These vegetation/fuel types are grassland, oak woodland, oak woodland/scrub oak, scrub oak, pitch pine, young plantation, and mature plantation (Figure 1), and they were used to assign fuel reduction methods for this study. Two additional land cover types that were not present in the 1995 aerial photographs used to delineate fuel types were added for this study. They were classified as a harrow land cover type type which included 7.5 hectares of former shrubland harrowed during spring 2002, and a burn land cover type occupying 3 hectares of forest burned in summer 1999. The harrow land cover type had very little canopy and was dominated by grasses, sedges, *Aster* spp., *Solidago* spp., and *Rubus* spp. The burn vegetation type also had a relatively open canopy but was dominated by shrubby forms of tree oak species such as *Q. velutina*, *Q. alba*, and *Q. stellata* as well as *Q. ilicifolia, Vaccinium* spp., *G. baccata, P. aquilinum*, and *C. peregrina*. It had large amounts of downed woody material and standing dead trees. Both the harrow and burn types represent disturbances that affect the habitats of rare insects.

Using Mouw’s (2002) fire behavior modeling and vegetation/fuel type classifications, an experimental firebreak expansion area was created to both widen an existing firebreak and examine the effects of fuel reduction techniques on fire behavior and larval *H. maia* habitat. Beginning in 2002, a 150-m-wide treatment area along an existing firebreak was established in the southwestern portion of the Forest. This area was dominated by three vegetation/fuel types of interest to fire managers (pitch pine, scrub oak, and oak woodland) and was located along both a road and bike trail, making it a potential ignition point. The pitch pine fuel type provides continuous flammable canopy that can lead to dangerous crown fire development. The scrub oak fuel type provides long open stretches of continuous flashy fuels that can increase the rate of spread of a surface fire. The oak woodland fuel type, containing densely stocked oak stems with leaves of lower combustibility, reduces the intensity of wind-driven fires, compared to pitch pine and scrub oak fuel types (Mouw 2002).

The goal of the treatments was to mechanically reduce the flammable fuels within the experimental area by breaking up the pitch pine canopy, reducing the height and continuity of flammable shrubs, and retaining the tree oaks to reduce the intensity of a wind-driven fire. Prescribed fire could then be used to assess the effectiveness of each treatment combination to alter fire behavior, as well as to examine the ability of fire to maintain this open fuel-reduced zone. Comparisons could also be made between characteristics of the habitat preferred by *H. maia* caterpillars across the Forest, and the habitats created by each of the treatment combinations, including a final prescribed burn.

Methods

Larval *Hemileuca maia* habitat

Because the larval stage of an insect's life is usually its most sedentary, and the stage in which most feeding and growth occur, impacts on larval habitats probably have the most immediate effect on a population (Ehrlich and Murphy 1987, Murphy et al.

1990, Tuskes et al. 1996, Young 1997). Thus, larval habitat variables were evaluated to determine how management activities altered *H. maia* habitats.

Twenty, 100-m-long transects were randomly located within each of the nine vegetation types (burn, harrow, grassland, oak woodland, oak woodland/scrub oak, scrub oak, pitch pine, young plantation, mature plantation) and searches were conducted along them to locate feeding clusters of *H. maia*. To locate larvae one observer walked transects in late June and early July 2003, noting all larval clusters within two meters of the transect. Surveys were conducted equally across all vegetation types rather than according to their representation on the landscape for two reasons: 1) to assess if such broad landscape-level characterizations of the vegetation could be used to delineate preferred habitats from aerial photographs; and 2) to avoid overlooking a correlation between larval presence and habitat variables in one of the less-well-represented or surveyed vegetation types due to small sample sizes.

All surveys were conducted by the same observer. When a larval cluster was discovered, its location was recorded using a Garmin GPS unit with an accuracy of 6 m (20 feet). Larval sites were characterized with respect to habitat variables later in the summer in order to focus survey efforts during the time period when *H. maia* larvae were most easily observed. To characterize habitat variables, a 225-m^2 (15 m x 15 m) plot was established, centered on the larval cluster or egg ring. This plot size provides an adequate representation of the plant species found in temperate forest/shrubland communities (Barbour et al. 1987). Habitat characteristics sampled included: 1) canopy cover, measured with a spherical densiometer, 2) height and percent cover of each of four vegetation strata (overstory, understory, high shrub, low shrub/herb) and height and percent cover of each plant species within each strata, both quantified on a Braun-Blanquet cover abundance scale (5 = 75-100%, 4 = 50-75%, 3 = 25-50%, 2 = 5-25%, 1 = 1-5%; [Mueller-Dombois and Ellenburg 2002]), and 3) size-class distribution and density of scrub oak (*Q. ilicifolia* and *Q. prinoides)* stems on a 1 m x 1 m subplot located at the center of the survey plot. From the cover/abundance data, "Cushing" importance values (IVs) (Clark and Patterson 1985) were calculated for *Q. ilicifolia* in order to transform cover/abundance information across physiognomic classes into a quantitative data set.

Ten 225-m^2 plots were also located randomly within each of the nine vegetation types throughout the forest for comparison with larval sites, for a total of 90 randomly selected plots. All of these plots were sampled as described above.

All variables measured with values in more than 10% of the total plots were evaluated using a principle components analysis (PCA) (McCune and Mefford, 1999). This was done to identify potential habitat variables that characterized *H. maia* sites. A correlation matrix was used to derive the principle components, as the unit of measurement differed among variables (McGarigal et al. 2000), and all variables were assessed for normality and transformed if necessary. Outliers were retained as they represented true ecological outliers, including two *H. maia* sites. Logistic regression analysis was then used to evaluate variables with the highest r^2 values on axes 1 and 2 as predictors of the presence of *H. maia* larvae across the nine vegetation types (SAS statistical software 9.1; SAS Institute 2004). Three variables identified as being of particular interest based on the biological needs of *H. maia* (canopy cover, scrub oak stem density, and *Q. ilicifolia* IV), were overlaid on the main PCA to assess the location of *H. maia* plots in multi-dimensional space relative to these factors and in relation to the randomly located plots.

Logistic regression analysis was then used to evaluate canopy cover, scrub oak stem density, and *Q. ilicifolia* IVs as predictors of the presence of *H. maia* larvae across the nine vegetation types (SAS statistical software 9.1; SAS Institute 2004). Results from the model were then used to evaluate experimental fuel-reduction plots with regard to their ability to provide habitat for *H. maia*.

Fuel reduction experiment

The goal of the fuel-reduction experiment was to evaluate the effectiveness of fuel-reduction techniques, other than harrowing, for creating fuel breaks while retaining or enhancing habitat characteristics upon which *H. maia* depends (Patterson et al. 2005). In 2002, twenty-four 45 m x 45 m (2025-m^2) treatment plots were created in three fuel types—pitch pine (PP), oak woodland (OW), and scrub oak (SO)—in the experimental firebreak expansion area (Figure 2). Three treatments (control, mow, mow/graze) were examined in both the oak woodland and scrub oak fuel types, and two treatments (control, thin/mow) were examined in the pitch pine fuel type. Individual treatments, each replicated three times, were randomly assigned to the experimental plots (Table 1) and put in place over two summers, 2002 and 2003. Treatments were:

- Control = no mechanical treatment (implemented in all three fuel types),
- Mow = shrub layers were mowed to a height of approximately 10 cm using a Rayco FM 225 flailmower/brush hog (both the oak woodland and the scrub oak fuel types received this treatment),

- Mow/Graze = shrub layers were mowed to a height of approximately 10 cm using a brush hog and then grazed by 8-9 sheep beginning at least 2 weeks post-mow to allow for shrub and herb regeneration, and continuing for 2-3 weeks until the majority of the low-lying vegetation was removed (both the oak woodland and the scrub oak fuel types received this treatment), and
- Thin/Mow = overstory pitch pines were thinned to a basal area of 5-7m^2/ha using a feller-buncher, then the shrub layers were mowed to a height of approximately 10 cm using a brush hog (only the pitch pine fuel type received this treatment).

The majority of fuels within the 150-m-wide experimental fuel reduction zone around the plots were treated with thinning of the pitch pines and mowing of the shrub layer to complete the fire break. Following fuels reduction, all 24 plots were burned in the spring of 2004 in order to document differences in fire behavior between treated and untreated conditions. The area around the treatment plots was burned in late winter 2004, to facilitate burning the experimental plots between 29 April and 7 May 2004.

The vegetation in the treatment plots was sampled in 2003 and 2004 to evaluate the effects of the various treatments, including burning. Habitat characteristics were sampled in the growing season following the treatments, after the vegetation had re-sprouted and attained its full growing season stature. Thus, vegetation characteristics measured in 2003 were the result of treatments in 2002, and the measurements taken in 2004 included the additional effects of burning. Because grazing occurred at the end of the growing season in 2003, vegetation sampling within the SO mow/graze plots did not include the second grazing effort, and no sampling was done in the OW mow/graze plots prior to burning in 2004. To relate habitats created by the treatments to larval *H. maia* habitat, vegetation was sampled on three randomly located 225-m^2 subplots in each 2025-m^2 experimental plot, and the means were calculated for each plot. Subplots were used rather than entire plots so that comparisons could more appropriately be made to the 225-m^2 larval plots. All subplots in the treatment area were sampled using the techniques described for plots centered on larval locations and randomly located plots within the vegetation types of MFCSF. Comparisons were then made between the vegetation parameters for the treatment sites and predictors of *H. maia* presence in the logistic regression model. Variable descriptions are presented as the mean ± SE.

T-tests were used to compare vegetation characteristics found to be important to *H. maia* on the larval plots (through logistic regression) with the same characteristics on treatment subplots. Treatments that produced vegetation similar to that found at *H. maia* locations were assumed to be beneficial to the moth.

Results

Larval *Hemileuca maia* habitat

Larvae of *H. maia* were found at 11 locations identified from 180 transects across MFCSF. Locations were in seven of the nine vegetation types (two each in harrow, grassland, oak woodland/scrub oak, and scrub oak; one each in burn, oak woodland, and young plantation; and none in mature plantation or pitch pine) suggesting that broadly classified vegetation types are not useful for identifying possible *H. maia* larval locations. The two vegetation types in which larvae were not found (pitch pine and mature plantation) were closed-canopy stands with little scrub oak.

From 35 variables the PCA identified three significant principle components, based on the “broken stick model” (McCune, Grace, and Urban 2002), of which only the first two explained >10% of the variance each (Table 2). Axis 1 was most strongly correlated with canopy cover, and Axis 2 was most strongly correlated with *Q. ilicifolia* IV (Appendix A). A color-coded graph of the PCA does not show *H. maia* sites in close association with any particular vegetation types (Figure 3). Grouping the nine vegetation types into three broader stand types (forested plots, shrub-dominated plots, and plots dominated by herbaceous plants) also did not show *H. maia* grouping closely with one broad stand type (Figure 4). Three of ten variables with the highest r^2 values on Axes 1 and 2 showed significance ($P<0.05$) in logistic regression (Appendix B). These variables were canopy cover, *Q. ilicifolia* IV, and overstory. Overstory and canopy cover were found to be highly correlated and thus redundant. Canopy cover, rather than overstory, was retained in subsequent analyses based on its potential biological significance for *H. maia*, as were *Q. ilicifolia* IV and scrub oak stem density.

Calculated mean and standard errors show that *H. maia* larvae were found in areas with little canopy cover (27.0 ± 7.1%), high scrub oak stem densities (20.2 ± 3.8 stems/m^2), and moderately high *Q. ilicifolia* IVs (4. 5 ± 0.7; Table 3; Appendix C). Of these three variables, only scrub oak stem density was a significant predictor of *H. maia* larval habitat, as determined using logistic regression ($P = 0.03$; Table 4).

The mean scrub oak stem density at the *H. maia* larvae sites was higher than the average stem densities found in all vegetation types, but not significantly higher than those found in scrub oak (18.3 ± 6.1 stems/m^2, P = 0.79) and grasslands (9.2 ± 4.6 stems/m^2, P = 0.08; Table 5).

Fuel reduction experiment

Three of the treatment combinations of 2002 and seven of the treatment combinations ending in prescribed burning in 2004 produced scrub oak stem densities similar to those found at *H. maia* larval sites (Tables 6 and 7). The 2002 treatment combinations most closely mimicking scrub oak densities of the larval sites were oak woodlands mow, scrub oak mow/graze, and scrub oak control (Table 6).

Nearly all of the treatment combinations that included burning produced mean scrub oak stem densities similar to those found at *H. maia* sites. Only the mean scrub oak stem densities of the burned pitch pine “control” plots were significantly different from those of the *H. maia* sites (Table 7). The oak woodland mow/graze/burn treatment produced marginally lower stem densities than found at *H. maia* locations (P = 0.06). The 2004 burning of the scrub oak plots, regardless of prior treatment, produced scrub oak stem densities higher than those found at *H. maia* larval sites (Table 7).

Discussion

Larval *Hemileuca maia* habitat

The discovery of *H. maia* larvae in seven of nine broadly classified vegetation types, but all in locations with similar characteristics at the 15m x 15m plot level, suggests that scale is an important factor for larval habitat delineation. *H. maia* larvae were found most often in plots having high scrub oak stem densities and other characteristics similar to those found in the scrub oak vegetation type (Table 3), but they were not found exclusively in that vegetation type as defined on a broad scale.

This suggests that *H. maia* are utilizing small patches of the scrub oak vegetation type defined at the plot level, within a variety of vegetation types defined at the landscape level. Plot-level characteristics may provide the best cues to females selecting oviposition sites that maximize the survival of her offspring. MNHESP (2004) and NatureServe (2004) have suggested that for survival of entire populations of *H. maia* for the long-term, hundreds of hectares of pitch pine-scrub oak barrens may be necessary. The results of this study suggest that such areas can be heterogeneous natural barrens communities including numerous patches of ideal oviposition sites, as adult *H. maia* can travel up to several kilometers between habitat patches (NatureServe 2004). The specialization of *H. maia* on barrens habitats in the Northeast—which are limited in their extent and proximity to one another—effectively limits the species' overall distribution in this region. The two vegetation types in which *H. maia* larvae were not found were pitch pine and mature plantation, vegetation types having the lowest mean scrub oak densities—the only variable showing statistical significance in the logistic regression analysis (Table 4).

The association of *H. maia* with dense scrub oak stems, regardless of vegetation type, likely has several explanations. In the Northeast, scrub oak is the primary food of the gregariously feeding larvae of this species, and higher densities of stems of the host plant could produce more leaves per unit volume and thus more food in a smaller space for growing larvae. Dense scrub oak stems could also provide more oviposition and resting sites, climate mediation, and even protection from predators and parasitoids that do not forage as well with increased complexity of vegetation structure (Stamp and Bowers 1988, Denno et al. 1990, Heinrich 1993, Montllor and Bernays 1993, Legrand

and Barbosa 2003). All of these factors can lead to higher survival rates in Lepidoptera (Stamp 1993).

Like other sprouting woody plants (Bond and Midgley 2001) scrub oaks increase stem density with disturbance and decrease stem density through self-thinning. Recently disturbed scrub oak plants re-sprout vigorously forming multi-stemmed, bushy plants, while undisturbed scrub oak stems become less dense as some stems enlarge and others die. These older undisturbed plants may be in areas that are succeeding to forest with the lack of disturbance, and thus the food plant is being reduced. Scrub oak and grassland are both vegetation types that experience regular disturbance, and both have scrub oak stem densities similar to those found at *H. maia* larvae sites. The scrub oak vegetation type includes large areas within frost bottoms where frost acts to prune the scrub oak (Motzkin et al. 2002), and the grassland vegetation type is mowed annually. Harrow and burn are two land cover types that also experienced disturbance, but they had scrub oak stem densities that were significantly different from those found at *H. maia* sites. The harrow vegetation type was recently disturbed using a method that removed scrub oak rootstocks, thus scrub oak stem densities were reduced. The burn vegetation type was disturbed in 1999 and is dominated by vigorously re-sprouting tree oak species that were dominant prior to the burn, rather than scrub oaks which are the preferred food of *H. maia*.

H. maia larvae may also be found in areas of high scrub oak stem densities due to microclimatic and physiological benefits. Larval Lepidoptera are widely known to be sensitive to changes in temperature and to have optimal species-specific thermal regimes (Casey 1993, Erhardt and Thomas 1991). Because insects do not metabolically thermoregulate to a significant degree, they depend on the environment to provide the heat needed to increase their metabolic rate (Casey 1993, Kingsolver and Woods 1997, Levesque et al. 2002). Within physiological limits, growth rates increase as larvae are exposed to higher temperatures, partly through increased food consumption and utilization efficiency. *H. maia* larvae hatch in early summer, before the highest daily air temperatures are reached. To maintain ideal metabolic temperatures, larvae are black, setae-covered, feed in a cluster, and “bask” in the sun to increase temperatures and subsequent developmental rates (Tuskes et al. 1996). They are known to utilize frost bottoms where the highest daily temperatures can be found during the summer (Goldstein 1997). Canopy-free, open scrub oak patches provide ideal basking conditions for heat-seeking caterpillars. Low, dense shrubs such as those found in disturbed areas also provide easier access to the ground for increased absorption of radiant heat.

Fuel reduction experiment

Overall, experimental plots having mean scrub oak stem densities closest to those found at *H. maia* larval sites were the scrub oak control plots, which had no mechanical treatments applied to them. This mirrors the finding that scrub oak plots randomly located across the Forest were most similar to *H. maia* larval sites in terms of mean scrub oak density (Table 5). The physical treatments that created mean scrub oak stem densities comparable to those found at *H. maia* larval sites were burning in oak woodland, mowing and then burning in oak woodland, and thinning followed by mowing and burning in pitch pine. Several other treatments (mowing in oak woodland, mowing then grazing in scrub oak, mowing then grazing and burning in oak woodland, burning in scrub oak, mowing then grazing and burning in scrub oak, and mowing then burning in scrub oak) created scrub oak stem densities similar to those found at *H. maia* sites, but the P-values were low and the variances high (Tables 6 and 7). Variances were generally higher in the treated plots than in the untreated plots. P-values developed from such small treatment sample sizes (N=3) and from means with such large variances should be interpreted with caution, as a small sample size could result in a lack of power to distinguish a difference between the treatments and the larval habitats. This could lead to the conclusion that the two entities are not different, when in fact differences may exist but not be detectable with only three treatment plots. Using an effect size of 12 (the difference in stem density needed to find statistical significance between the *H. maia* sites and the different vegetation types using a t-test), power of 0.8 by convention, and the smallest variance found in the treatment plots not significantly different from *H. maia* sites, (36.1), a power analysis for two-sample t-test determined that a minimum sample size of 5 would be necessary to have enough power to detect a significant scrub oak stem density difference.

This study suggests that to provide habitat for the larval stage of *H. maia*, areas of moderately high scrub oak stem densities (20.18 ± 3.83 stems/m^2) should be maintained at least in patches across an extensive barrens landscape. Appropriate stem densities can be determined by counting numbers of stems on 1 m x 1 m square plots. Visual assessments can be used to identify likely areas of appropriate density, with sampling used to confirm suitable *H. maia* habitat. The existing scrub oak and grassland vegetation types at MFCSF appear to provide the needed habitat characteristics for this species, but oak woodlands and pitch pine stands can also be manipulated to provide similar scrub oak stem densities. Oak woodland areas can be burned or mowed and burned to provide habitat, while pitch pine stands need to be thinned before mowing and burning. Canopy closure in these stands is still much higher than found at *H. maia* sites, which could make basking more difficult for larvae. Maintaining persistent, high-density scrub oak might also be difficult in these areas without additional treatment to the canopy. Treatments in these forested communities create scrub oak stem densities that are similar to those found at *H. maia* sites, but they are not permanent and require additional disturbance to prevent self-thinning to original stem densities.

Long-term use of these fuel reduction techniques may produce habitat features not observed in this three-year study. For example, repeated mowing or grazing over a number of years can reduce shrub cover and favor more herbaceous plants. Frequent treatments—especially fire—run the risk of preventing colonization of the management area through continuous destruction of animals. Growing season burns can reduce shrub densities and delay regeneration relative to dormant season burns (Patterson et al. 1983, Dunwiddie et al. 1997). Studies of longer duration or continued monitoring in these treatment areas over time will add to our understanding of the long-term changes to potential *H. maia* habitat.

These results show that fuels management can provide habitat for one of the regionally rare insect species found there at MFCSF. The results of the analysis of *H. maia* habitat characteristics can guide managers in their attempts to provide habitat for this species while reducing fire danger. However, we cannot assume that the habitat needs of one sandplain insect species are representative of the needs of other rare insect species found in this system. Nearly all of the regionally rare insect species found at MFCSF require a native barrens community with an open vegetation structure (NatureServe 2004). An open system can be maintained by active management but there is no one management technique or treatment interval that will provide the ideal habitat for all species (Swengel 2001, Swengel and Swengel 2001, Panzer and Schwartz 2002, Wagner et al. 2003). All of these species are vulnerable to mortality from habitat management at some part of their lives, so management protocols should be implemented to maintain a patchwork of habitats in time and space to allow recolonization of treated areas.

Table 1: Treatment history for the southwest experimental fuel break study at MFCSF.

Fuel Type	Treatment	Plot	2002 Treatment	2003 Treatment	2004 Treatment
Pitch Pine	Control	1	--	--	Burn (April)
		5	--	--	Burn (May)
		9	--	--	Burn (April)
	Thin/Mow	2	Thin (July)/Mow (July)	--	Burn (May)
		3	Thin (July)/Mow (July)	--	Burn (May)
		7	Thin (July)/Mow (July)	--	Burn (May)
Oak Woodland	Control	2	--	--	Burn (April)
		7	--	--	Burn (April)
		8	--	--	Burn (April)
	Mow/Graze	1	Mow (July)	Graze (July)	Burn (April)
		5	Mow (July)	Graze (June-July)	Burn (April)
		9	Mow (July)	Graze (August)	Burn (April)
	Mow	3	Mow (July)	--	Burn (April)
		4	Mow (July)	--	Burn (April)
		6	Mow (July)	--	Burn (April)
Scrub Oak	Control	4	--	--	Burn (May)
		5	--	--	Burn (May)
		8	--	--	Burn (May)
	Mow/Graze	1	Mow (July)/Graze (August)	Graze (September)	Burn (May)
		2	Mow (July)/Graze (September)	Graze (September)	Burn (May)
		9	Mow (July)/Graze (September)	Graze (September)	Burn (May)
	Mow	3	Mow (July)	--	Burn (May)
		6	Mow (July)	--	Burn (May)
		7	Mow (July)	--	Burn (April)

Table 2: Cross-products matrix containing correlation coefficients among structural variables. First three axes are significant based on broken-stick eigenvalues, and explain 43% of the variance.

Axis	Eigenvalue	% of Variance	Cumulative % of Variance	Broken-stick Eigenvalue
1	6.188	17.679	17.679	4.147
2	5.822	16.635	34.314	3.147
3	3.072	8.778	43.092	2.647
4	2.294	6.556	49.648	2.313
5	2.071	5.916	55.564	2.063
6	1.731	4.945	60.509	1.863
7	1.556	4.445	64.954	1.697
8	1.257	3.590	68.545	1.554
9	1.070	3.058	71.603	1.429
10	1.032	2.949	74.552	1.318

Table 3: Description of habitat variables (mean ± SE) measured at *H. maia* locations and in nine vegetation types on Martha’s Vineyard, MA.

Site Type	Canopy Closure (% closure)	Scrub Oak Stem Density (#/m^2)	*Q. ilicifolia* Importance Value
H. maia	27.00 ± 7.11	20.18 ± 3.83	4.45 ± 0.72
Grassland	37.27 ± 7.34	9.20 ± 4.55	1.30 ± 0.40
Oak Woodland	75.85 ± 5.24	1.70 ± 0.60	3.40 ± 0.31
OW/SO	59.45 ± 5.51	6.90 ± 1.60	5.80 ± 0.33
Scrub Oak	26.56 ± 8.55	18.30 ± 6.13	5.40 ± 0.56
Young Plantation	74.84 ± 7.64	5.40 ± 3.47	2.90 ± 0.84
Mature Plantation	86.24 ± 3.66	0.10 ± 0.10	0.60 ± 0.31
Pitch Pine	81.51 ± 3.38	1.00 ± 0.67	2.40 ± 0.69
Harrow	9.68 ± 3.83	5.50 ± 2.30	0.90 ± 0.31
1999 Burn	20.11 ± 3.11	3.70 ± 0.47	6.70 ± 3.11

Table 4: Logistic regression analysis of habitat variables important in predicting *H. maia* larvae presence. Scrub oak stem density (bold) was a significant predictor variable (p = 0.05).

Parameter	df	Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square
Canopy closure	1	-0.022	0.014	2.408	0.121
Scrub oak importance value	1	0.199	0.158	1.575	0.210
Scrub oak stem density	1	0.052	0.024	4.599	**0.032**

Table 5: An analysis of scrub oak stem densities at *H. maia* locations compared to each of nine vegetation types at MFCSF. Stem densities that are significantly different (p = 0.05) are indicated by p-values in bold type.

Site Type	N	Mean	SE	Variance	t-statistic	df	p-value
H. maia site	*11*	*20.18*	*3.83*	*161.36*	--	--	--
Grassland	10	9.20	4.55	206.61	-1.86	19	0.079
Oak Woodland	10	1.70	0.60	3.57	4.77	10.49	**0.001**
OW/SO	10	6.90	1.60	25.66	3.20	13.35	**0.007**
Scrub Oak	10	18.30	6.13	375.78	0.27	19	0.793
Young Plantation	10	5.40	3.47	119.62	2.82	19	**0.011**
Mature Plantation	10	0.10	0.10	0.10	5.24	10.01	**0.000**
Pitch Pine	10	1.00	0.67	4.44	4.93	10.60	**0.001**
Harrow	10	5.50	2.30	52.94	3.29	16.18	**0.005**
1999 Burn	10	3.70	0.47	96.46	-2.70	19	**0.014**

Table 6: A comparison of scrub oak stem densities at *H. maia* larvae sites with those on experimental plots, following 2002 treatment with measurements taken in 2003. Means that are significantly different (p = 0.05) are indicated by p-values in bold type.

Site Type	N	Mean	SE	Variance	t-statistic	df	P-value
H. maia site	*11*	*20.18*	*3.83*	*161.36*	--	--	--
PP-Control	3	4.89	2.28	15.59	3.43	11.27	**0.005**
PP-Thin/Mow	3	5.22	1.39	5.81	3.67	11.79	**0.003**
OW-Control	3	3.11	1.56	7.26	4.13	11.95	**0.001**
OW-Mow	3	9.67	4.19	52.78	1.85	5.90	0.114
SO-Control	3	20.67	5.55	92.33	-0.06	12	0.953
SO-Mow/Graze	3	35.33	12.68	482.11	-1.59	12	0.139
SO-Mow	3	62.89	10.28	316.93	-4.79	12	**0.000**

Table 7: A comparison of scrub oak stem densities found at *H. maia* larvae sites with those on experimental plots, following 2004 controlled burns, with measurements taken in summer 2004. Means that are significantly different (p = 0.05) are indicated by p-values in bold type.

Site Type	N	Mean	SE	Variance	t-statistic	df	P-value
H. maia site	11	20.18	3.83	161.36	--	--	--
PP-Control/Burn	3	4.67	2.91	25.44	3.23	9.32	**0.010**
PP-Thin/Mow/Burn	3	12.22	7.02	148.04	0.97	12	0.352
OW-Control/Burn	3	18.33	11.10	369.44	0.20	12	0.843
OW-Mow/Graze/Burn	3	9.00	3.47	36.11	2.16	7.59	0.064
OW-Mow/Burn	3	13.11	7.31	160.48	0.86	12	0.409
SO-Control/Burn	3	66.33	23.86	1707.44	-1.91	2.10	0.190
SO-Mow/Graze/Burn	3	61.33	15.07	681.33	-2.65	2.26	0.104
SO-Mow/Burn	3	36.11	11.84	420.26	-1.71	12	0.113

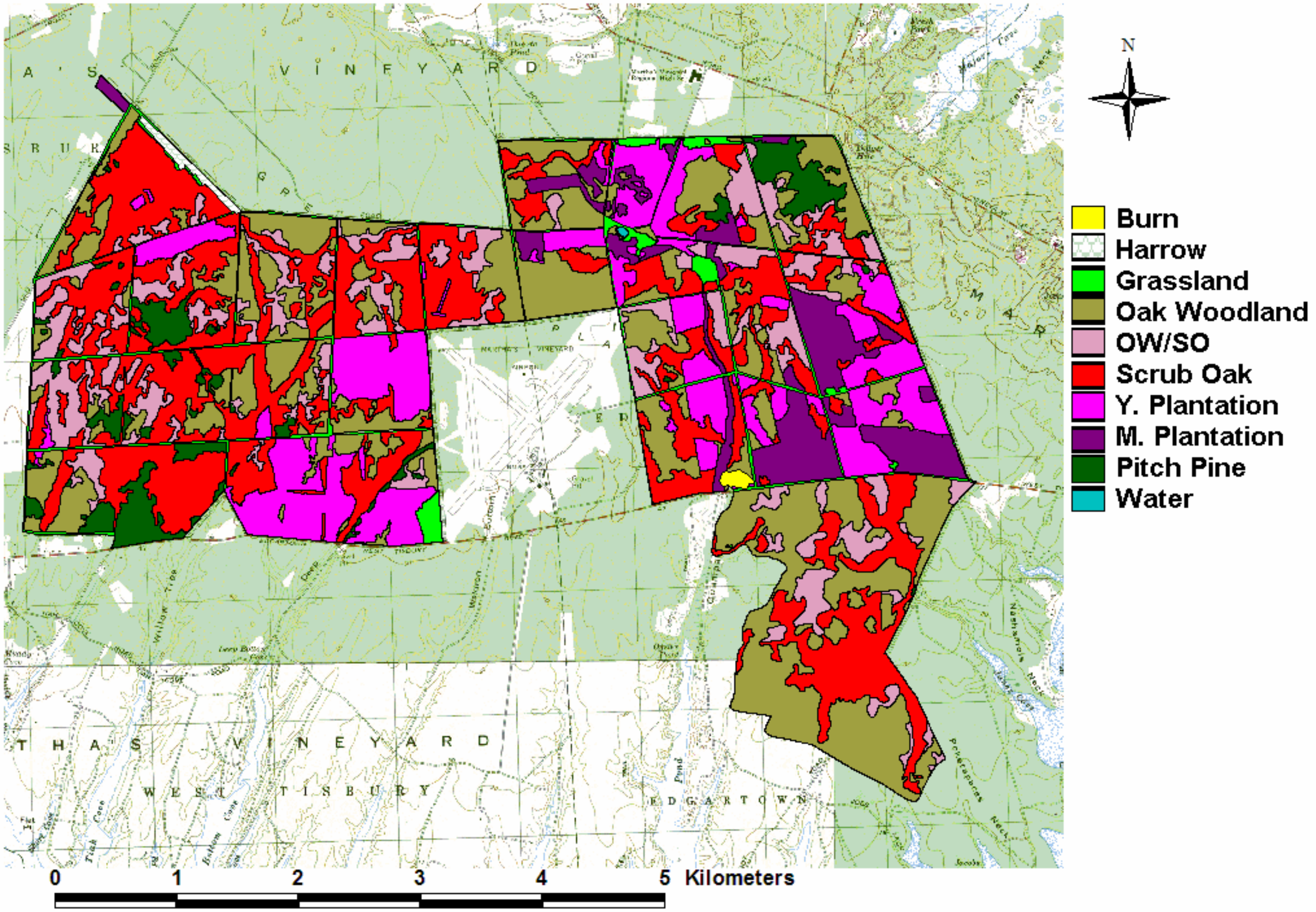

Figure 1: Vegetation or fuel types at MFCSF based on aerial photography and vegetation sampling (adapted from Mouw 2002).

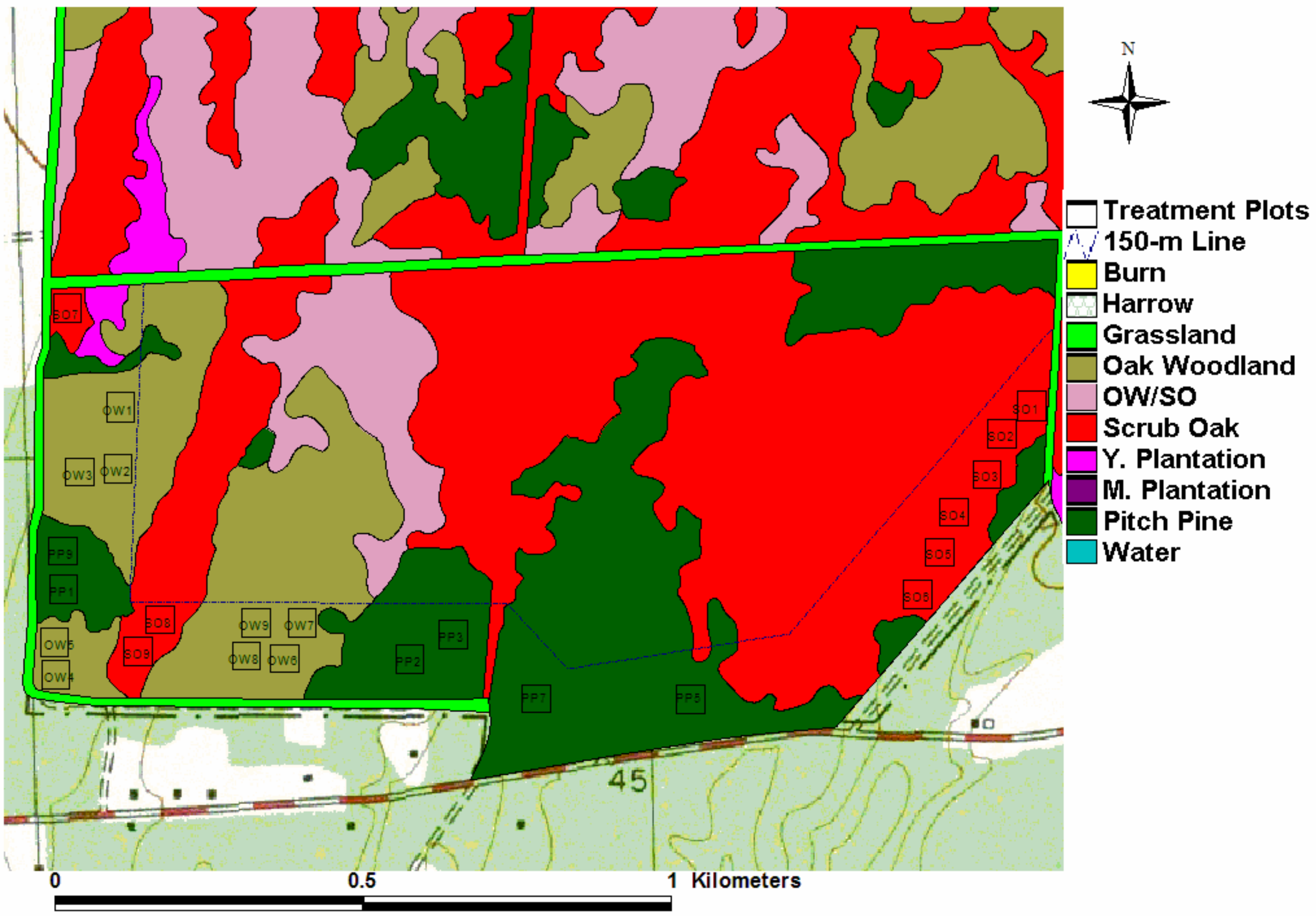

Figure 2: Twenty-four 45m x 45m (half-acre) experimental fuel reduction plots in three vegetation types in SW corner of MFCSF.

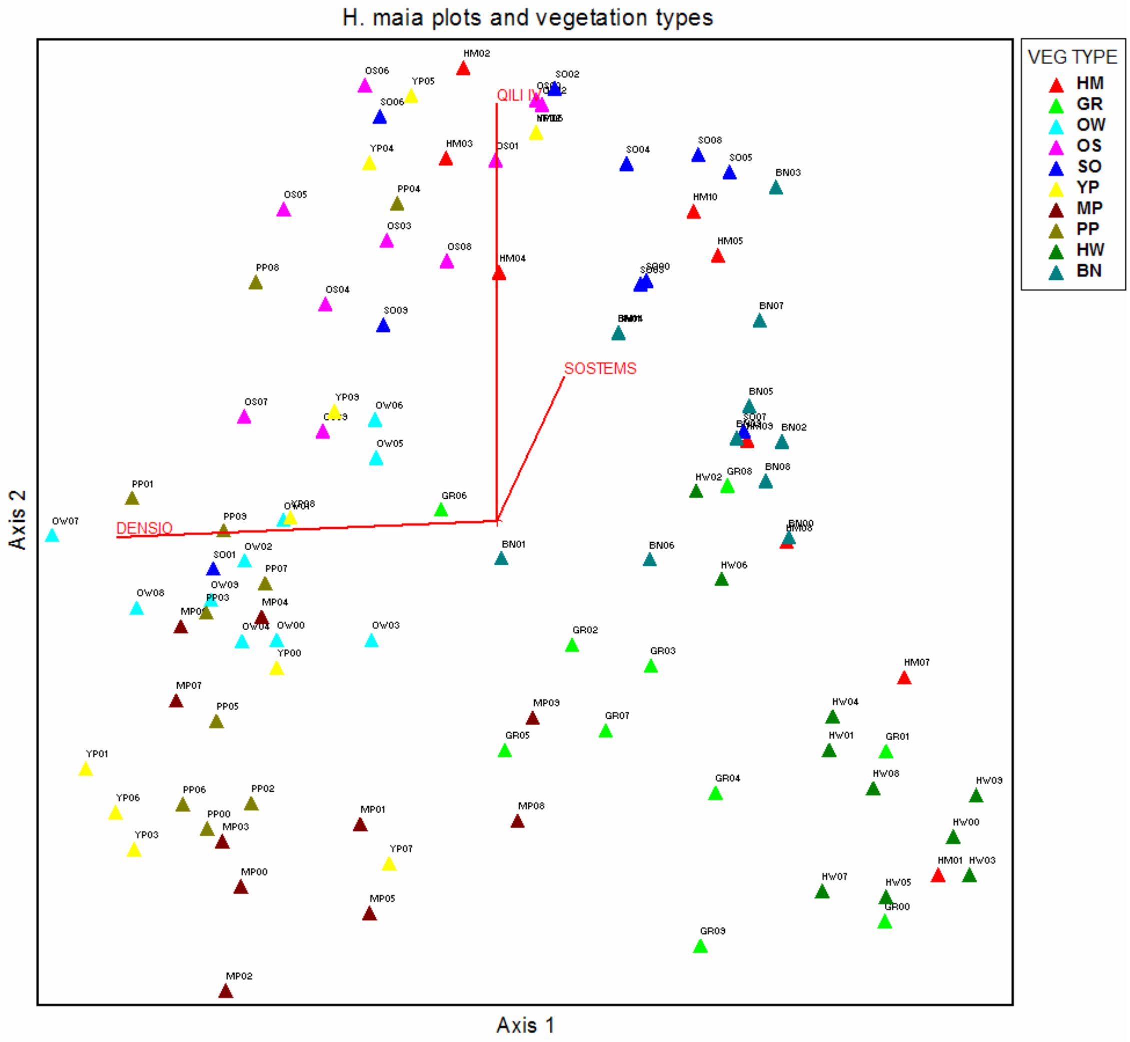

Figure 3: Principle Components Analysis of 35 variables representing the vegetation composition at 11 *H. maia* locations (HM) and 90 plots randomly located in nine vegetation types (GR = grassland, OW = oak woodland, OS = oak woodland/scrub oak, SO = scrub oak, YP = young plantation, MP = mature plantation, PP = pitch pine, HW = harrow, BN = burn) across MFCSF.

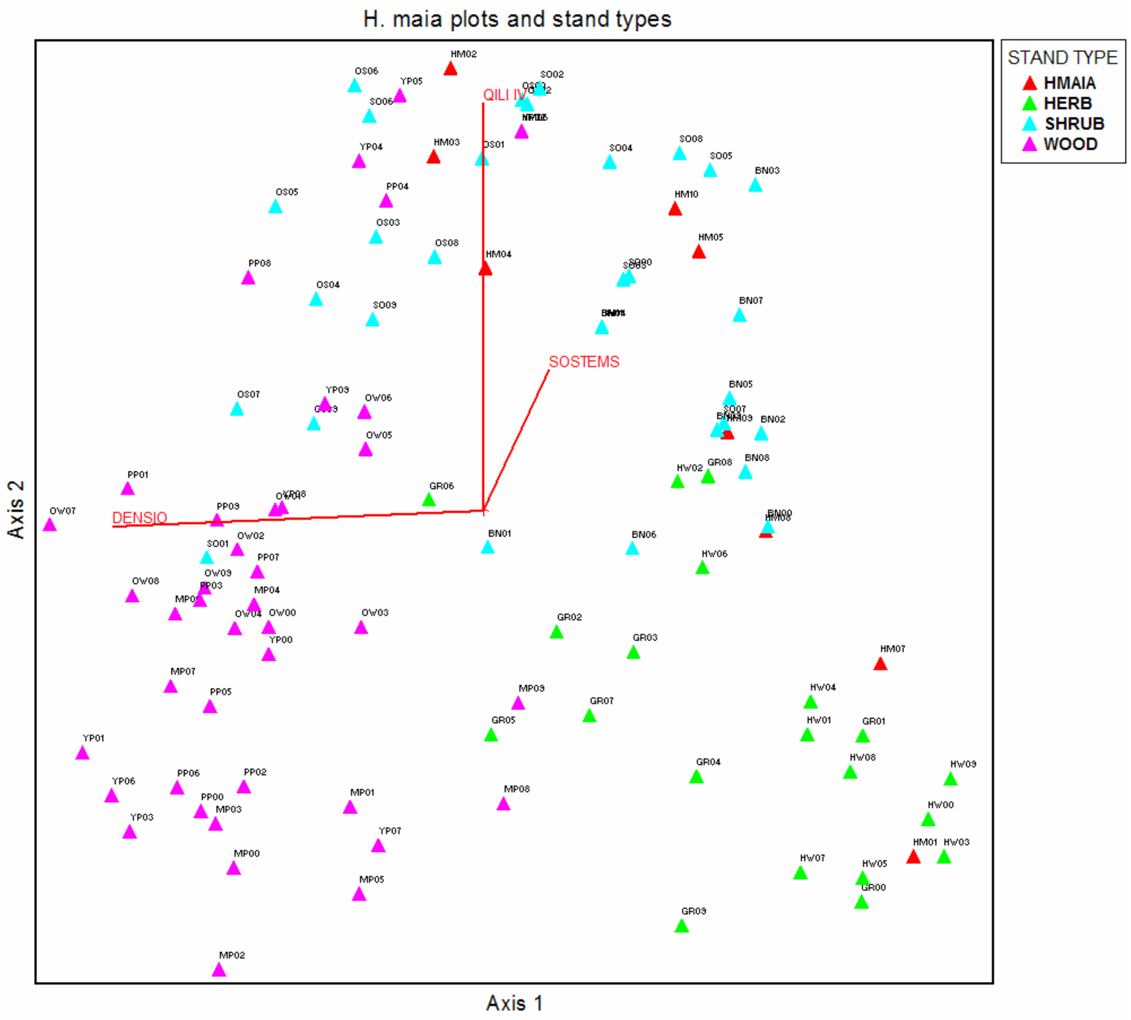

Figure 4: Principle Components Analysis of 35 variables representing the vegetation composition at 11 *H. maia* locations (HMAIA) and 90 plots randomly located and grouped into three broad stand types (HERB = plots dominated by herbaceous vegetation, SHRUB = shrub-dominated plots, WOOD = forested plots) across MFCSF.

CHAPTER 3

EFFECTS OF HOST PLANT CHOICE ON LARVAL DEVELOPMENT OF *HEMILEUCA MAIA* (LEPIDOPTERA: SATURNIIDAE)

Introduction

Larval host plant selection and utilization play important roles in the survival and fecundity of Lepidoptera (Cunningham et al. 2001, Awmack and Leather 2002). Caterpillars may be generalist herbivores or be very host specific, and host plant specificity can vary from region to region even for the same species. This variability may be the result of a local adaptation to a combination of host plant availability, interspecific competition, predation and parasitism pressures, and local and regional climatic variation (Haukioja 1993, Heinrich 1993, Montllor and Bernays 1993, Stamp 1993, Parry et al. 2001). Structural components of the larval host plant, which can be altered by disturbance and which can affect growth and predation rates, can also impact the survival and fecundity of Lepidoptera (Legrand and Barbosa 2003).

Hemileuca maia (Drury) is known to feed heavily on tree oak species in the southern parts of its range, but appears to be restricted to scrub oak species in the northeastern U.S. (Martinat et al. 1996, Tuskes et al. 1996, Wagner et al. 2003). Scrub oaks, like *Q. ilicifolia* and *Q. prinoides,* remain as shrubs even in maturity, rarely attaining heights much over two meters. Tree oak species such as *Q. alba*, *Q. stellata*, and *Q. velutina* usually reach heights over five meters at maturity. At the Manuel F. Correllus State Forest (MFCSF) on Martha's Vineyard, Massachusetts, *H. maia* larvae feed almost exclusively on *Q. ilicifolia* and *Q. prinoides* and do not appear to use the extensive mature oak forests. However, early instar *H. maia* larvae will occasionally feed on tree oak species if they are in the shrub layer and structurally similar to the preferred scrub oaks (personal observation, G. Boettner, personal communication).

The physical structure of host plants has been linked to insect survival, and that structure can be altered through disturbance. Disturbances such as herbivory, cutting, or burning often induce sprouting in many deciduous species, (Bond and Midgley 2001) leading to greater morphological complexity. Legrand and Barbosa (2003) show that greater architectural complexity—e.g., increased branching that develops in many re-sprouting shrubs after a disturbance—decreases the ability of a predator to find prey on the vegetation. Heinrich (1993), Montllor and Bernays (1993), and Denno et al. (1990) suggest that predators and parasitoids strongly influence the adaptive landscape of host plant selection. Increased numbers of leaves in re-sprouting shrubs provide more food in a smaller space for growing larvae, which could benefit gregariously feeding species like *H. maia*. Increased morphological complexity of prospective host plants may also provide more oviposition and resting sites, or provide climate mediation.

Lacking the ability to significantly metabolically thermoregulate, insects depend on the environment to provide heat for activity and growth (Casey 1993, Kingsolver and Woods 1997, Levesque et al. 2002). *H. maia* larvae hatch in early summer, before the highest air temperatures are reached for the year. They are black, setae-covered, cluster-feeding caterpillars that "bask" in the sun which increases body temperature and subsequent developmental rates. Low, dense shrubs such as those found in open disturbed areas provide easier access to the radiant heat given off by the ground as well as access to the tops of plants for basking, without necessitating lengthy travel through shaded portions as would occur on a taller shrub or tree. Stamp and Bowers (1988) determined that lower temperatures, such as those found in shaded portions of a host plant, significantly increased development time of *H. lucina* larvae.

Nutritional quality plays an important role in host plant selection as well. The consumption of highly nutritious leaves can lead to larger pupae and higher fecundity in *Hemileuca* species (Foil et al. 1991). Qualities such as high nutrient levels, low levels of anti-herbivore chemicals, high water content, and soft tissue may allow caterpillars to grow more quickly and form larger pupae (Feeny 1970, Ayres and MacLean 1987, Foil et al. 1991, Casey 1993, Dussourd 1993, Slansky 1993, Dudt and Shure 1994, Kingsolver and Woods 1997, Levesque et al. 2002). It has been suggested that passing quickly through the larval stage and into the pupal stage decreases vulnerability to predators and parasitoids (Casey 1993). The short growing season found at the northern edge of this species' range could also limit host plant selection. An insect species may evolve host plant utilization based on whether it can complete the larval stage before nutritional degradation or senescence of the host plant (Slansky 1993).

At MFCSF, *H. maia* appears to prefer areas with high scrub oak stem densities, a trait associated with previous site disturbance (see Chapter 1). Of 11 *H. maia* larval clusters discovered along randomly located transects at MFCSF in 2003, eight were found in areas that showed obvious signs of previous disturbance from mowing, burning, harrowing, or vehicle use (Haggerty, unpublished data) and the average height of the scrub oaks on which they fed was one meter. This species, evolving in a disturbance-dependent system at the northern edge of its range, may have become dependent on the prolific, multi-stemmed scrub oak species that are typical of sandplains in the Northeast.

To determine if the preference of *H. maia* to feed almost exclusively on scrub oaks rather than on tree oak species in New England is related to leaf quality, comparisons were made in a laboratory setting. Growth rates and pupal weights were compared for *H. maia* larvae raised on leaves of *Q. ilicifolia*, leaves of *Q. prinoides*, leaves of *Q. stellata*, and leaves of *Q. alba*. To ascertain if there was a difference in leaf quality of *Q. ilicifolia* due to disturbance, growth rate and pupal weight were compared between *H. maia* caterpillars fed leaves from plants at previously disturbed and undisturbed sites.

To determine if the apparent preference of *H. maia* for disturbed rather than undisturbed *Q. ilicifolia* plants was related to microclimate differences, comparisons were also made in the field. Growth rates and pupal weights were compared between *H. maia* larvae raised on previously disturbed and undisturbed *Q. ilicifolia* plants at the same site. Predation and parasitism were controlled using protective rearing sleeves.

Materials and Methods

Study Site

Martha’s Vineyard is an island of roughly 22,000 hectares located approximately 8 kilometers southeast of mainland Massachusetts. It has a mild maritime-influenced coastal New England climate. The Manuel F. Correllus State Forest (MFCSF) is located in the center of the island and covers over 2000 hectares of barrens vegetation and conifer plantations. Barrens vegetation—including grasslands, heathlands, shrublands, oak savannahs, and pitch pine-scrub oak barrens—are found in the northeastern part of the United States where the glacially-derived soils are coarse, well-drained, and nutrient-poor. At MFCSF, natural plant communities cover nearly 75% of the Forest, the remainder comprised of manmade communities of grassy firelanes (4%) and conifer plantations (21%). The native vegetation communities found at MFCSF include scrub oak plains (31.5%), oak woodlands (26.7%), oak savannahs within stretches of scrub oak (12.3%), and pitch pine (*Pinus rigida*) forests (4.5%) (Mouw 2002). Scrub oaks are *Quercus* species which grow as shrubs, only occasionally reaching over 2 meters in height. *Quercus ilicifolia* is the dominant scrub oak species at MFCSF and it often grows in tall, dense thickets in frost bottoms and other canopy-free areas. *Quercus prinoides* is less common than *Q. ilicifolia* and is most often found in the low shrub layer (0-1 meters tall). Tree oak species at MFCSF include *Q. alba, Q. stellata,* and *Q. velutina,* and they are found in both the understory (2-5 m tall) and overstory (>5 m tall).

Open-structure or early-seral communities such as the “barrens” communities found on sandplains in the Northeast, require frequent disturbance or grass, shrub and forb vegetation will be overgrown by taller, woody vegetation (Motzkin et al. 1996, Dunwiddie et al. 1997, Goldstein 1997, Motzkin and Foster 2002). Early successional plant communities found on sandplains were historically maintained through a variety of disturbances such as fire, heavy frost (especially in low areas), and salt spray and wind from ocean storms near the coast (Foster and Motzkin 1999, Griffiths and Orians 2004). These areas are prone to wildfire because barrens vegetation produces abundant, flammable fuel that decomposes slowly on the dry soils. Frost bottoms occur where cold air pools in topographic depressions within the otherwise flat sandplains. These depressions, in meltwater channels or kettle holes left by retreating glaciers, can experience freezing temperatures in any month of the year. Only a few tolerant plant species, such as scrub oaks and some grassland and heathland species, can survive there (Barbour et al. 1998, Motzkin et al. 2002). Without trees there is no canopy to retain radiant heat after sunset, nor an overstory to shade the frost bottom after sunrise. This creates a highly dynamic temperature regime leading to delayed leaf-out on plants in the frost bottom, and the pruning of scrub oaks by late season frosts (Aizen and Patterson 1995, Goldstein 1997, Motzkin 20002). At MFCSF, fire suppression and the introduction of cold-tolerant trees into low areas have removed some of the effects of traditional disturbances, while harrowing, mowing, and vehicle use have created new disturbance patterns.

Field experiments examining the effects of prior *Q. ilicifolia* disturbance on *H. maia* growth rates and pupal weights were conducted at various locations in MFCSF, where adjacent areas of disturbed and undisturbed *Q. ilicifolia* could be easily accessed. A "disturbed" area of *Q. ilicifolia* was defined as an area at least two m in diameter that was dominated by *Q. ilicifolia* less than one meter tall, and found within an extensive area of *Q. ilicifolia* $\geq$ 0.5 m taller than the disturbed patch. Only sites where the source of disturbance was easily identifiable were used in order to avoid using sites where unknown forces altered *Q. ilicifolia* growth and could affect *H. maia* development. Sources of disturbances at the experimental sites were mowing, frost, and vehicle use (i.e., old roads).

Laboratory experiments were conducted at the MFCSF headquarters in the northeastern portion of the Forest. Ambient temperatures inside the building ranged from 15° and 25° C throughout the summer of 2004.

Methods

H. maia egg rings were located at MFCSF on 8 and 9 May 2004, and brought indoors prior to hatching (24 May 2004 from the uplands and 8 June 2004 from the frost bottoms). Egg rings were placed inside clear plastic cups with lids to prevent loss of larvae upon hatching. Within 12 hours of hatching early instar larvae were separated into treatment groups and placed in either the field or laboratory feeding groups. Because *H. maia* larvae feed gregariously as early instars, groups of caterpillars were the sample units rather than individual larvae.

Laboratory Experiment

Within 12 hours of hatching, ten larvae were placed inside each lidded, transparent plastic cup with freshly cut foliage, for each of five treatments per egg ring. Six egg rings were divided this way for a total of 30 cups with ten caterpillars per cup. The five treatments were:

- D = “disturbed” *Q. ilicifolia* (foliage clipped from *Q. ilicifolia* found within a previously disturbed area as defined above),
- U = “undisturbed” *Q. ilicifolia* (see above),
- P = *Q. prinoides* (foliage clipped from this scrub oak species),
- S = *Q. stellata* (foliage clipped from overhead branches of this tree oak species), and

- A = *Q. alba* (foliage clipped from overhead branches of this tree oak species).

The appropriate foliage was collected from MFCSF and changed every 1-2 days, and the different host plant types were gathered from the same general location (roughly within a 50 m radius) on a given day. All foliage gathered had approximately the same leaf size to reduce the possible effect of leaf age on caterpillar growth. Frass was removed from the rearing cups when the vegetation was changed. To prevent overcrowding, as larvae grew the groups were divided into two groups of five and then divided again into two groups of two or three per original treatment cup; this treatment mimicked the natural splitting of groups that occurs in the field as larvae grow and disperse. Molt dates were recorded. Cup locations were rotated in order to avoid effects of location within the room. After the fourth molt at least five cm of sterile peat were placed in the bottom of each cup as a pupation substrate. Foliage continued to be changed and frass removed until all caterpillars in each cup had pupated. Pupation dates were recorded. In late August all pupae were removed from the substrate, sexed, and weighed on a Mettler balance, accurate to 0.001 g. Pupae were then returned to scrub oak habitat at MFCSF.

Comparisons were made between mean pupal weights of each treatment group in the laboratory setting using ANOVA (SAS 9.1, 2004). Because pupal and adult *H. maia* vary in size by sex (females are significantly larger than males), comparisons were made within gender groups. Foil et al. (1991) also found significant differences in pupal weights based solely on familial group, so family groups (egg rings) were used as a blocking variable in ANOVA.

Comparisons were made between development rate of each treatment group in a laboratory setting using ANOVA (SAS 9.1, 2004). Familial and gender differences can also be found in growth rates (Foil et al. 1991); females spend several days longer as larvae and continue feeding before pupation, which creates the size difference described above. However, larvae of *H. maia* tend to molt synchronously within familial feeding groups prior to the final molt when sex differences emerge. For this reason, and because *H. maia* larvae cannot be sexed without destruction, development rate was determined by calculating the number of days needed to transition from a hatchling to a fifth instar larva. Analysis of variance was used to analyze time to fifth instar, using egg ring as a blocking variable. Variable descriptions are presented as the mean ± SE.

Field Experiment

Eighty caterpillars from each egg ring were randomly divided into two groups of 40 and placed at a single location in the field within 12 hours of hatching. Twelve different sites were used across the forest, nine in the uplands and three in a frost bottom. Because of a delay in leaf emergence and subsequent *H. maia* hatch dates within frost bottoms (Aizen and Patterson 1995, G. Boettner, unpublished data), larvae placed in the frost bottom were from egg rings found in frost bottoms, and larvae placed in uplands were from egg rings found in uplands. At each site, 40 caterpillars were placed on a *Q. ilicifolia* shrub within a “disturbed” area as defined earlier, and 40 larvae from the same egg ring were placed on a *Q. ilicifolia* shrub in the adjacent “undisturbed” scrub oak. “Disturbed” and “undisturbed” shrubs were always within five meters of one another, and care was taken to avoid placing either group on the disturbance interface. Larvae were placed on branches containing leaves of roughly the same size for both treatments to reduce potential effects of leaf age on caterpillar growth. To prevent loss of larvae due to predation, parasitism, and wandering, each group of 40 was enclosed within a fine-mesh rearing sleeve placed over the branch of the food plant and tied at both ends. Rearing sleeves were checked daily and frass was removed as needed. When food within the rearing sleeve became depleted, each group was moved to a new branch of the appropriate type ("disturbed" or "undisturbed") within the same area. To prevent overcrowding, groups were divided into two groups of 20, and then four groups of 10 as the larvae grew. Sleeves were replaced as necessary. Molt dates were noted, as well as losses to predators that breached the protective sleeves. Several days after the fourth molt, larvae were placed inside large plastic lidded containers with at least two inches of peat and freshly cut *Q. ilicifolia* branches from their appropriate treatment type. Original groups were retained, so up to 40 individuals were contained in each box. Boxes were then placed in an outbuilding at the headquarters of MFCSF and larvae were fed fresh foliage every 1-2 days as necessary until all larvae had pupated. Frass was removed from boxes with changes of foliage. Pupation dates were recorded. In late August all pupae were removed from the substrate, sexed, and weighed on a Mettler balance, accurate to 0.001 g. Pupae were then returned to scrub oak habitat at MFCSF.

Comparisons were made between mean pupal weights of each treatment group using paired t-tests (SAS 9.1, 2004). Mean pupal weights were analyzed within gender groups to remove the effects of sexual dimorphism. Numbers of days between hatch and fourth molt (into fifth instars) for each treatment group were also analyzed using paired t-tests (SAS 9.1, 2004). Variable descriptions are presented as the mean ± SE.

Results

Hemileuca maia eggs gathered on 24 May 2004 from upland locations hatched between 28 May 2004 and 2 June 2004. Eggs gathered from the frost bottom on 8 June 2004 hatched between 9 and 10 June 2004. The average number of larvae hatched per egg ring was 90.

Laboratory Experiment

Blocking for family relationship (egg ring), treatment did not have a significant effect on mean pupal weight (F = 1.55, P = 0.226 for females and F = 1.00, P = 0.437 for males). There did appear to be a trend toward lower pupal weights in larvae fed *Q. prinoides* although this trend was not statistically significant (Tables 8 and 9).

Treatments did have a significant effect on development rate (F = 3.47, P = 0.026) when blocked by egg ring. *Hemileuca maia* larvae fed *Q. alba* and *Q. prinoides* required the longest time to reach the fifth instar (34.50 days ± 0.99 each) while those fed *Q. ilicifolia*—“undisturbed” or “disturbed”—required the shortest time (33.00 ± 0.68 and 33.17 ± 0.98 respectively). Using Tukey’s yardstick, however, only the larvae reared on undisturbed *Q. ilicifolia* leaves grew significantly faster than those reared on *Q. prinoides* and *Q. alba*.

A 20% mortality rate was experienced in the laboratory setting, mostly as a result of mold and disease due to unusually high humidity during the summer of 2004.

Field Experiment

Mean pupal weights of larvae reared on undisturbed and previously disturbed *Q. ilicifolia* showed no significant difference (t = 2.08, P = 0.061 for females and t = 1.81, P = 0.097 for males), although there was a trend towards higher pupal weights in larvae reared on undisturbed *Q. ilicifolia* if higher p-values were considered (Table 10). There were no discernible differences in the number of days required to reach the fifth instar (t = -0.42, P = 0.681).

The mortality rate of larvae in the field was 31% due to predation by birds (*Coccyzus americanus, Phasianus colchicus,* etc.), mammals (mice and/or voles), vespid wasps, spiders, ants, and pentatomid hemiptera. Predation rates between treatments were not assessed as the presence of the rearing sleeves in both disturbed and undisturbed scrub oak likely altered natural predator search images.

Discussion

Laboratory Experiment

Quercus spp. did not influence the mean pupal weights of *H. maia* in the laboratory, suggesting that the nutritional and chemical make up of the host plant is not the most critical variable driving pupal weight gain and thus fecundity in this system.

The trend in larvae of both sexes to have lower mean pupal weights when fed *Q. prinoides* was unexpected since *H. maia* commonly feeds on *Q. prinoides* at MFCSF. *Quercus prinoides* is found predominantly in the low shrub layer between 0 and 1 meter in height. It also tends to be most common in areas receiving the heaviest frost, such as openings within *Q. ilicifolia* thickets where grassland and heathland plants can gain a foothold (personal observation). After a late frost in the growing season (12 June 2004 for example), a distinct pattern of frost-killed leaves is apparent in the scrub oak dominated areas: leaves on shrubs below one meter tend to survive the frost while leaves above that point—where most *Q. ilcifolia* leaves are found—are killed. Solitary tree oaks in open oak savannah also tend to lose many leaves to late frosts while plants near the ground, like *Q. prinoides*, are mostly spared. Since *H. maia* hatches in late May through early June at MFCSF, late frosts that kill most *Q. ilicifolia* leaves would virtually eliminate the primary food of *H. maia* in certain areas. At these times *Q. prinoides* would still have leaves and could provide enough food for *H. maia* larvae to survive until *Q. ilicifolia* puts out a new flush of leaves. Thus, even though feeding on *Q. prinoides* does not result in the highest *H. maia* pupal weights, it may still be a critical food source in frost-prone areas at MFCSF.

The significant effect of host plant on development rate supports the larval choice of *Q. ilicifolia* as the primary food source, as well as the suggestion that *Q. prinoides* is not an optimum food plant for *H. maia*. In this case it appears that *Q. ilicifolia*, in an undisturbed state at least, may be nutritionally superior to two of the other *Quercus* species tested, or *H. maia* has adapted locally to optimize nutrient extraction from *Q. ilicifolia*. This short development time may be a critical factor in determining survival at the northern edge of this species' range, thus leading to the host specificity found here.

Field Experiment

There was a marginally significant difference between the mean pupal weights of *H. maia* larvae grown in previously undisturbed *Q. ilicifolia* plants compared to those grown on nearby disturbed *Q. ilicifolia* plants. Those reared on undisturbed plants were slightly larger than those reared on previously disturbed plants, if a p-value of 0.10 is considered. This runs counter to the observation that *H. maia* larvae seem to be found most often on previously disturbed *Q. ilicifolia* plants. There are a number of possible causes for this discrepancy. The design of the experiment may have altered the microclimate or behavior of the *H. maia* larvae such that they were able to grow to a larger size on the undisturbed plants. For example, the rearing sleeves used in the experiment may alter the temperatures larvae experience, may reduce wind speeds in the taller undisturbed plants, and may remove the ability of the larvae to move about on the plant in search of optimal temperature and leaf quality.

The lack of treatment effect could also be related to the alteration of predation and parasitism rates which are thought to shape phytophagous arthropod foraging patterns in many systems (Stamp and Bowers 1988, Stamp and Bowers 1991, Stamp 1993, Lill et al. 2002, Murphy 2004, Singer et al. 2004). The rearing sleeves protected *H. maia* larvae from parasitism, as no larvae were found to be parasitized. This lack of parasitism is nearly impossible to find in unprotected systems (Boettner et al. 2000, Tuskes et al. 1996). Rearing sleeves did not, however, completely protect larvae from predators. There was a 31% loss of larvae due to avian, mammalian, and arthropod predation with all sites receiving some predation. The most effective predators appeared to be vespid wasps, who chewed through the protective mesh and killed the caterpillars inside, and pentatomid hemipterans, who preyed upon caterpillars through the mesh when caterpillars were close to it. Predators attacked rearing sleeves on both disturbed and undisturbed *Q. ilicifolia* plants equally as vespid wasps may have developed a search image for the rearing sleeves (Richter 2000). For comparison, 40 larvae were placed at each of six additional sites but were left unprotected from predators and parasitoids. Of those, two groups were reduced by 50% within three days, and the evidence at the sites suggested that they were preyed upon by vespid wasps. All larvae were missing from these sites within 12 days. Larvae at two other sites were preyed upon by pentatomid hemiptera and were all absent from the site within 22 days. Larvae at only two sites reached their third molt (although their numbers were reduced by well over 50% by then) at which point *H. maia* feeding groups often disperse. Larvae had disappeared from these sites within 28 days. In the wild, *Hemileuca* larvae may find protection from predators and parasitoids by escaping into the interior of the host plant (Stamp and Bowers 1988). Vespid wasps, which can have a significant effect on *Hemileuca* larvae survival (Stamp and Bowers 1988, Stamp and Bowers 1991), use visual cues in their hunting strategy and often return to areas of previous hunting success (Richter 2000). Predators and parasitoids that hunt in flight may selectively prey upon caterpillars higher in the shrub and forest layers. Larvae feeding on shorter, bushier, previously disturbed shrubs of *Q. ilicifolia* may be outside the main search image of the dominant predators and parasitoids, and larvae may be more protected from predators within the higher morphological complexity of the bushier plants (Stamp and Bowers 1988, Legrand and Barbosa 2003). Future studies into the effects of predation and parasitism on *H. maia* populations at MFCSF would help us understand not only the pressures that shape insect populations, but may offer insight into regional host plant selectivity as well.

Larval duration for *H. maia* was the same on both previously disturbed or undisturbed plants, reinforcing the laboratory findings between these two treatments. In the controlled laboratory experiments larvae fed *Q. prinoides* and *Q. alba* took longer to reach the fifth instar than those grown on *Q. ilicifolia*, but disturbance was unimportant.

It would appear that host plant selection for *H. maia* in the Northeast is driven at least in part by the nutritive properties of the host plants. Early instar *H. maia* larvae feed almost exclusively on scrub oaks (*Q. ilicifolia* and *Q. prinoides*) in the Northeast, but feed on any number of tree oaks in the southern part of their range. This study suggests that the growth rate sustained on a particular host plant species may play a role in the selection of *Q. ilicifolia* as the main host plant for *H. maia* at MFCSF. Insects at the northern limit of their range may be confined by the short growing season of potential host plants, and by the cooler temperatures that limit their own growth potential. The selection of *Q. ilicifolia* as the primary host plant at MFCSF may be associated with the fact that growth rates were higher on this species than on the other *Quercus* species tested, but only significantly higher than *Q. prinoides* and *Q. alba*. *Quercus prinoides*, even with its poor performance in the growth rate and pupal weight tests, may be an important host plant for *H. maia* during late season frosts when *Q. ilicifolia* and tree oaks are defoliated.

The apparent preference of *H. maia* to feed on *Q. ilicifolia* that has been previously disturbed may be related to external factors not tested in this experiment. Predation and parasitism can play very strong roles in shaping host plant selectivity and may play a role in the regionally narrow host plant selection of *H. maia* in the sandplains of the Northeast. Further studies into predation and parasitism rates on scrub oak that has had a prior disturbance, compared to undisturbed scrub oak could offer a better understanding of host plant selection for *H. maia* and other Lepidopteran species at the northern limits of their range.

Table 8: Means (± SE) of time from hatch to fifth instar (days) and pupal weight (g) of *H. maia* reared on leaves from five different host plant treatments (*Q. ilicifolia* from a previously disturbed site [D], *Q. ilicifolia* from a previously undisturbed site [U], *Q. prinoides*, *Q. stellata*, and *Q. alba*).

Treatment	Days to 5th Instar mean ± SE	Pupal Weight (g) mean ± SE	
		Female	Male
Q. ilicifolia (U)	33.00 ± 0.68	1.43 ± 0.08	1.05 ± 0.04
Q. ilicifolia (D)	33.17 ± 0.98	1.47 ± 0.07	1.06 ± 0.04
Q. prinoides	34.50 ± 0.99	1.30 ± 0.08	0.98 ± 0.04
Q. stellata	33.83 ± 1.01	1.41 ± 0.05	1.02 ± 0.05
Q. alba	34.50 ± 0.99	1.49 ± 0.06	1.02 ± 0.03

Table 9: Analysis of variance blocked by family group (2-way ANOVA $P < 0.05$) of the effects of five different host plant treatments (*Q. ilicifolia* from a previously disturbed site [D], *Q. ilicifolia* from a previously undisturbed site [U], *Q. prinoides*, *Q. stellata*, and *Q. alba*) on time from hatch to fifth instar (days) and pupal weight (g) by sex of *H. maia*.

Source	df	F ratio	P-value
Days to 5th Instar	4	3.47	0.026
Female Pupal Weight	4	1.55	0.226
Male Pupal Weight	4	1.00	0.437

Table 10: Paired t-test for means (± SE) of time from hatch to fifth instar (days) and pupal weight (g) by sex (F = female, M = male) of *H. maia* reared in the field on previously undisturbed (U) and disturbed (D) *Q. ilicifolia* plants at MFCSF.

Treatment group	Undisturbed *Q. ilicifolia* (U)	Disturbed *Q. ilicifolia* (D)	Mean difference (U-D)	T-value	P-value
F Pupal Weight (g) mean ± SE	1.28 ± 0.03	1.21 ± 0.05	0.08	2.08	0.061
M Pupal Weight (g) mean ± SE	0.98 ± 0.03	0.91 ± 0.03	0.07	1.81	0.097
Days to 5th instar mean ± SE	29.75 ± 0.37	30.00 ± 0.65	-0.25	-0.42	0.681

CHAPTER 4

CONCLUSION

Scale is an important consideration in defining *Hemileuca maia* habitat as the characteristics of landscape level vegetation classifications apply best at the plot level, and do not necessarily define habitat at the landscape level. The sites where *H. maia* larval clusters were found met the description of the scrub oak vegetation type, but they were not found exclusively in that vegetation type as defined on a broad scale. This suggests that *H. maia* may be utilizing scrub oak habitat patches within the broader heterogeneous landscape of MFCSF. MNHESP (2004) and NatureServe (2004) suggest that for survival of entire populations of *H. maia* for the long-term, hundreds of hectares of pitch pine-scrub oak barrens may be necessary. Within MFCSF, high scrub oak stem density is a significant factor in determining habitat suitability and the scrub oak and grassland vegetation types provide the preferred scrub oak stem densities. High stem densities could provide higher densities of leaves to feed dense clusters of caterpillars, climate mediation, and protection from predators and parasitoids.

A number of experimental fuel reduction techniques produced high scrub oak stem densities. These include mowing in oak woodlands, mowing and grazing in oak woodlands, and all burning except in untreated pitch pine stands. However, many of these treatments produced stem densities well above the range of those found at *H. maia* sites or anywhere else on the Forest. The suitability of areas with such high stem densities as *H. maia* habitat is uncertain. Over time, densities in these areas will likely decline through natural self-thinning and approach those found at *H. maia* sites. The long-term effects of the treatments on potential *H. maia* habitat is also unclear, as this study examined the habitats created by each treatment within one year of implementation. Effects of these treatments over time and effects of long-term use of these techniques may create very different habitats than those examined here. Longer term studies and studies of the direct impact of fuels management on rare insect populations would enhance our understanding of these species and the effects of land management on their populations.

Alteration to the habitat of *H. maia* at the northern extent of its range can also have different effects than in other areas. In the Northeast, *H. maia* feeds almost exclusively on scrub oaks but utilizes numerous tree oak species in the southern part of its range. The shorter growing season in the north may limit host plant use to those species that allow it to complete develop before nutritional degradation and senescence of the host plant. The discovery that *H. maia* larvae have higher growth rates on *Q. ilicifolia* compared to local tree oak species supports this suggestion. However, the indication that *H. maia* takes longer to reach the fifth instar when reared on *Q. prinoides* (a preferred host plant on MFCSF) suggests that the use of this plant in the northeast may relate more to its persistence in frost-prone areas where *Q. ilicifolia* may be defoliated and thus unavailable as food during the larval period. There was no difference in pupal weights (an indication of future egg production) between larvae fed on different host plants, suggesting that the host plant preference in this case is more a function of increased survival rather than increased fecundity.

Nine of the 11 sites where *H. maia* larvae were found along random transects were at locations showing evidence of previous disturbance. The fact that rearing *H. maia* larvae on previously disturbed and undisturbed *Q. ilicifolia* plants led to no difference in growth rate or pupal weight, and in fact seemed to indicate a slight tendency towards higher pupal weights on undisturbed plants, may be related to the presence of rearing sleeves in this experiment. These sleeves may alter microclimate and larval behavior and in particular, protect them from predators and parasitoids. Tri-trophic interactions may significantly impact phytophagous insect populations and can even drive host plant selection (Stamp and Bowers 1988, Stamp and Bowers 1991, Stamp 1993, Richter 2000, Lill et al. 2002, Murphy 2004, Singer et al. 2004).

Understanding the underlying mechanisms behind host plant selection and habitat utilization is crucial to habitat management for phytophagous insects. Land management impacts on rare insect habitat go beyond just the direct effects on the quantity of host plants in an area. Host plant structure and the mosaic of habitat patches on the landscape play important roles in the success or failure of local insect populations.

APPENDIX A

Abbreviations used for variable names in the Principle Components Output from PC-ORD Version 4.27 (Appendix B)

DENSIO – canopy cover measured with a spherical densiometer
SOSTEMS – scrub oak stem density
QILI IV – *Q. ilicifolia* importance value
OVERSTORY – overstory vegetation stratum
UNDERSTORY – understory vegetation stratum
HISHRUB – high shrub vegetation stratum
LOSHRUB – low shrub vegetation stratum
OSPINRIG – *Pinus rigida* in the overstory vegetation stratum
OSPINSTR – *Pinus strobus* in the overstory vegetation stratum
OSPINRES – *Pinus resinosa* in the overstory vegetation stratum
OSQUEALB – *Quercus alba* in the overstory vegetation stratum
OSQUESTE – *Quercus stellata* in the overstory vegetation stratum
OSQUEVEL – *Quercus velutina* in the overstory vegetation stratum
USQUEALB – *Quercus alba* in the understory vegetation stratum
USQUESTE – *Quercus stellata* in the understory vegetation stratum
USQUEVEL – *Quercus velutina* in the understory vegetation stratum
USQUEILI – *Quercus ilicifolia* in the understory vegetation stratum
HIQUEALB – *Quercus alba* in the high shrub vegetation stratum
HIQUESTE – *Quercus stellata* in the high shrub vegetation stratum
HIQUEVEL – *Quercus velutina* in the high shrub vegetation stratum
HIQUEILI – *Quercus ilicifolia* in the high shrub vegetation stratum
HIGAYBAC – *Gaylussacia baccata* in the high shrub vegetation stratum
LOQUEALB – *Quercus alba* in the low shrub vegetation stratum
LOQUESTE – *Quercus stellata* in the low shrub vegetation stratum
LOQUEILI – *Quercus ilicifolia* in the low shrub vegetation stratum
LOQUEPRI – *Quercus prinoides* in the low shrub vegetation stratum
LOVACSPP – *Vaccinium spp.* in the low shrub vegetation stratum
LOGAYBAC – *Gaylussacia baccata* in the low shrub vegetation stratum
LOKALANG – *Kalmia angustifolia* in the low shrub vegetation stratum
LOPTEAQU – *Pteridium aquilinum* in the low shrub vegetation stratum
LOCOMPER – *Comptonia peregrina* in the low shrub vegetation stratum
LORUBUS – *Rubus spp.* in the low shrub vegetation stratum
LOGRASSEDGE – Grasses and sedges in the low shrub vegetation stratum
LOMOSSLICHEN – Mosses and lichens in the low shrub vegetation stratum
LOASTERACEA – *Aster spp.* and *Solidago spp.* in the low shrub vegetation stratum

APPENDIX B

PRINCIPLE COMPONENTS OUTPUT FROM PC-ORD Version 4.27
H. maia plots and Random Points within Vegetation Types

```
            VARIANCE EXTRACTED, FIRST 10 AXES
        ------------------------------------------------------------
                                           Cumulative   Broken-stick
     AXIS   Eigenvalue   % of Variance    % of Var.     Eigenvalue
     ---------------------------------------------------------------------
      1       6.188          17.679        17.679          4.147
      2       5.822          16.635        34.314          3.147
      3       3.072           8.778        43.092          2.647
      4       2.294           6.556        49.648          2.313
      5       2.071           5.916        55.564          2.063
      6       1.731           4.945        60.509          1.863
      7       1.556           4.445        64.954          1.697
      8       1.257           3.590        68.545          1.554
      9       1.070           3.058        71.603          1.429
      10      1.032           2.949        74.552          1.318
     ---------------------------------------------------------------------
```

```
                          FIRST 6 EIGENVECTORS
------------------------------------------------------------------------------------
                   Eigenvector
variables              1          2          3          4          5          6
------------------------------------------------------------------------------------
DENSIO            -0.3645    -0.0786    -0.0283     0.0822    -0.0518     0.0223
SOSTEMS            0.1536     0.2307    -0.0875     0.0814    -0.0901    -0.0697
QILI IV           -0.0089     0.3935     0.0002     0.0282     0.0164    -0.1180
OVERSTOR          -0.3171    -0.1134    -0.1284     0.2090     0.0368     0.0778
UNDERSTO          -0.2104     0.0745     0.0158    -0.4698    -0.1501     0.0071
HISHRUB           -0.0561     0.3215    -0.0101    -0.0576     0.0113    -0.1421
LOSHRUB            0.0801     0.1138     0.1575    -0.1089     0.5069     0.0514
OSPINRIG          -0.1568    -0.0043    -0.1367    -0.0702     0.2019     0.3487
OSPINSTR          -0.0892    -0.1401    -0.0984     0.2039    -0.4778     0.1162
OSPINRES          -0.0930    -0.0841    -0.0852     0.0056    -0.1974    -0.1359
OSQUEALB          -0.2153    -0.0928     0.1161     0.2575     0.2499    -0.2130
OSQUESTE          -0.0609     0.1463    -0.1177     0.0417     0.0553     0.1553
OSQUEVEL          -0.1816    -0.0903     0.0104     0.0027     0.1148     0.1983
USQUEALB          -0.1745    -0.0678     0.1888    -0.2784    -0.1301    -0.1683
USQUESTE          -0.1330     0.1629    -0.1129    -0.3130     0.0073     0.0767
USQUEVEL          -0.1321    -0.0505     0.2202    -0.4374    -0.1020     0.0473
USQUEILI          -0.0826     0.1290    -0.0944    -0.1572    -0.1344    -0.0531
```

```
HIQUEALB   -0.0916    -0.0233     0.3727     0.0702    -0.0656    -0.3478
HIQUESTE   -0.0043     0.1427     0.0201     0.0386    -0.0432     0.3943
HIQUEVEL    0.0091     0.0172     0.4030    -0.1432    -0.1404     0.1760
HIQUEILI   -0.0517     0.3584     0.0884    -0.0022     0.0564    -0.0928
HIGAYBAC   -0.1954    -0.0777     0.0087    -0.0923     0.2152     0.1093
LOQUEALB   -0.0130    -0.0322     0.3259     0.1002     0.0527    -0.2774
LOQUESTE    0.1991    -0.0303     0.2254     0.0423    -0.0471     0.3297
LOQUEILI    0.0408     0.3389    -0.0160     0.1159    -0.0079    -0.0824
LOQUEPRI    0.0943     0.2996    -0.1178     0.0543    -0.0416     0.0308
LOVACSPP   -0.2084     0.0554     0.2152     0.0771     0.0651     0.0720
LOGAYBAC   -0.2697     0.0853     0.1597     0.1484     0.2734     0.1260
LOKALANG   -0.0163     0.2201    -0.1754    -0.0963    -0.0009    -0.0488
LOPTEAQU    0.1321     0.1503     0.2634     0.0555    -0.0561     0.1525
LOCOMPER    0.2277     0.0074     0.2301    -0.0212    -0.0347     0.1941
LORUBUS     0.2124    -0.1458    -0.0427    -0.1435     0.1606    -0.0841
LOGRASSE    0.2632    -0.1897    -0.0604    -0.1259     0.1363    -0.0544
LOMOSSLI    0.1402     0.0388     0.2406     0.1873    -0.1793     0.1625
LOASTERA    0.2703    -0.1827    -0.1095    -0.1555     0.1839    -0.0893
--------------------------------------------------------------------------------------------

variables = 35

                    COORDINATES (SCORES) OF plots
------------------------------------------------------------------------------------------------
                        Axis (Component)
    plots                  1          2          3          4          5          6
------------------------------------------------------------------------------------------------
   1 HM01             4.4740    -3.3331    -1.1731    -1.1856     1.2087    -0.3884
   2 HM02            -0.3492     4.2674    -1.7484    -0.4511     0.6545    -0.4513
   3 HM03            -0.5194     3.4236    -0.7566    -0.4495    -0.1478    -0.6685
   4 HM04             0.0226     2.3435    -0.4040     1.3878     0.5913     0.8868
   5 HM05             2.2375     2.5072    -0.8974     0.9324    -0.5885    -0.8417
   6 HM06             0.3999     3.6562    -1.7659    -1.6962    -1.5495    -1.7366
   7 HM07             4.1274    -1.4712     0.4695     0.3125    -0.5290     0.5402
   8 HM08             2.9366    -0.1923    -1.4118    -0.5294     0.6091    -0.7465
   9 HM09             2.5341     0.7653     0.8873    -0.2258     0.7461     0.4505
  10 HM10             1.9883     2.9129     1.3411     1.4277    -0.1125    -1.9560
  11 HM11             1.2270     1.7783     2.1345     2.2922    -1.6462     2.7948
  12 GR00             3.9338    -3.7688    -1.6315    -1.4810     1.5014    -1.0969
  13 GR01             3.9373    -2.1600    -0.7051    -0.3296     0.2105    -0.3164
  14 GR02             0.7530    -1.1654     0.2199    -1.8472    -0.6892     1.5269
  15 GR03             1.5602    -1.3571     2.4008     1.9678    -0.3694     1.2587
  16 GR04             2.2155    -2.5554    -0.0091    -2.0319     0.7619     0.2081
  17 GR05             0.0719    -2.1535    -0.8486     2.3119    -2.3391     0.8331
  18 GR06            -0.5677     0.1101     1.7515    -2.8494    -1.1052    -0.9846
  19 GR07             1.1035    -1.9712    -1.3776     0.0904     1.0047     0.7293
```

20 GR08	2.3309	0.3340	-0.2703	0.6796	-0.4506	0.8159
21 GR09	2.0669	-3.9882	-0.1507	0.0702	1.9785	-2.4873
22 OW00	-2.2395	-1.1174	1.2673	2.0047	1.7100	-1.6160
23 OW01	-2.1698	0.0099	0.5572	1.8218	1.4778	0.3335
24 OW02	-2.5636	-0.3703	2.0976	2.5727	1.2331	-2.7323
25 OW03	-1.2734	-1.1231	-0.4105	0.9064	1.2367	0.2754
26 OW04	-2.5915	-1.1350	0.1360	1.7524	2.0821	0.4544
27 OW05	-1.2316	0.5949	0.3271	2.1418	1.1128	-2.1286
28 OW06	-1.2377	0.9609	1.6848	0.7931	0.6951	-1.6719
29 OW07	-4.5160	-0.1258	2.4986	-3.9519	0.2353	0.9349
30 OW08	-3.6639	-0.8167	2.5289	0.4452	0.5100	-2.1457
31 OW09	-2.9103	-0.7350	0.1068	0.5386	1.4837	-0.6678
32 OS00	0.3947	3.9613	-1.3600	1.0127	0.3080	-0.6150
33 OS01	-0.0158	3.3950	-1.1041	0.0185	-0.3611	0.1744
34 OS02	0.4580	3.9139	-1.9363	-1.6073	-0.4002	0.0371
35 OS03	-1.1159	2.6454	0.3818	1.2933	0.8714	-0.0040
36 OS04	-1.7386	2.0420	-0.0592	0.8008	1.0739	-1.0375
37 OS05	-2.1723	2.9381	0.7421	-0.0338	0.3695	-0.3861
38 OS06	-1.3448	4.1031	-2.1671	-1.0284	0.4244	-0.2584
39 OS07	-2.5622	0.9961	-0.1881	-2.2334	0.4759	1.6183
40 OS08	-0.5054	2.4446	-1.9757	-0.5086	-0.6700	-1.1272
41 OS09	-1.7624	0.8475	2.1755	2.4583	1.2007	-2.9289
42 SO00	1.5081	2.2609	-1.7506	-0.2808	-0.4759	-0.7435
43 SO01	-2.8852	-0.4474	1.8514	-4.4566	-0.2005	0.8470
44 SO02	0.5821	4.0750	-0.6923	-0.0016	0.1495	-0.8460
45 SO03	1.4528	2.2343	-1.0014	-0.6897	-0.3785	-1.2632
46 SO04	1.3157	3.3654	-0.4768	0.1087	-1.3099	-0.7891
47 SO05	2.3543	3.2872	-0.0665	0.9009	-0.8601	-0.6627
48 SO06	-1.1947	3.8114	-1.6060	-0.5809	-0.2572	0.8106
49 SO07	2.4940	0.8545	-1.3793	0.4714	0.3023	-0.9334
50 SO08	2.0374	3.4499	-0.8725	0.4070	-0.2910	-1.0179
51 SO09	-1.1554	1.8485	-0.9794	0.7551	0.6470	-0.9894
52 YP00	-2.2382	-1.3805	1.5725	1.4261	1.7026	-2.3912
53 YP01	-4.1764	-2.3321	-0.2293	-0.2445	-1.2769	-0.2312
54 YP02	0.3999	3.6562	-1.7659	-1.6962	-1.5495	-1.7366
55 YP03	-3.6839	-3.0899	0.6875	1.2957	0.6822	-0.8762
56 YP04	-1.2988	3.3746	-1.8270	0.0126	0.4294	1.4373
57 YP05	-0.8750	4.0115	-1.6686	-1.4168	-0.6010	0.1023
58 YP06	-3.8751	-2.7470	-0.8182	0.3310	1.3251	0.2687
59 YP07	-1.0950	-3.2166	-2.6590	2.2427	-4.6863	0.5123
60 YP08	-2.0987	0.0350	-2.8431	-1.1790	-0.8380	1.9835
61 YP09	-1.6520	1.0346	-1.6122	0.3407	-0.2997	0.1643
62 MP00	-2.6001	-3.4385	-0.7191	-1.2572	-4.8420	-1.2316
63 MP01	-1.3878	-2.8496	-1.4187	1.8796	-2.2796	0.0853
64 MP02	-2.7498	-4.4179	-1.9058	2.6573	-4.5408	-0.9722
65 MP03	-2.7917	-3.0121	-0.3352	0.9993	-1.1691	1.0061

```
   66 MP04      -2.3867   -0.9007   -0.3069   -0.9168   -0.6481    2.5846
   67 MP05      -1.2933   -3.6887   -2.4306    2.1628   -4.4721    0.1824
   68 MP06      -3.2131   -0.9944    4.4968   -4.0378   -2.7869   -2.4456
   69 MP07      -3.2611   -1.6874    2.2019   -3.6992   -1.0186   -1.7295
   70 MP08       0.2051   -2.8193   -1.7280    0.2923   -1.3126   -1.0727
   71 MP09       0.3635   -1.8442    0.1175   -0.9709   -0.7665    0.3472
   72 PP00      -2.9405   -2.8940   -0.8094    1.3332    2.6195    1.1729
   73 PP01      -3.7095    0.2144   -0.5768   -2.1159    1.8288    1.9149
   74 PP02      -2.5003   -2.6517   -0.9909    1.1903    2.3777    0.9649
   75 PP03      -2.9595   -0.8638   -0.8969   -0.0412    1.9737    2.0033
   76 PP04      -1.0184    2.9890   -0.7544    1.1240    1.3177    1.6295
   77 PP05      -2.8428   -1.8766   -0.1739    0.2842    1.5879    0.9633
   78 PP06      -3.1911   -2.6651   -0.5612    1.5329    2.4926    1.5696
   79 PP07      -2.3513   -0.5845   -0.2739   -1.0874    0.6696    1.3495
   80 PP08      -2.4440    2.2541   -0.8495   -1.6069    0.9935    1.3318
   81 PP09      -2.7738   -0.0828   -0.4925   -2.1820    0.0038    1.5765
   82 HW00       4.6216   -2.9754    0.4828   -1.5010    0.6441    0.8540
   83 HW01       3.3608   -2.1550   -1.5632   -0.7012    0.6976   -1.0527
   84 HW02       2.0098    0.2811   -0.6378    0.6660    0.5324    0.0012
   85 HW03       4.7850   -3.3281   -0.5686   -1.3578    1.3042   -0.0525
   86 HW04       3.4008   -1.8403   -0.4437   -0.1244   -0.2608    0.4831
   87 HW05       3.9472   -3.5320   -1.2485   -1.3684    1.2933   -0.7847
   88 HW06       2.2765   -0.5439   -1.0383   -0.1392    0.2201    0.9130
   89 HW07       3.2918   -3.4813   -1.5237   -1.1710    1.1727   -0.9411
   90 HW08       3.8115   -2.5168   -0.9109   -0.6594    0.7425    0.0983
   91 HW09       4.8581   -2.5736   -0.4721   -1.0757    0.8069    0.0545
   92 BN00       2.9580   -0.1486    1.6528    0.4206   -0.0611    0.2505
   93 BN01       0.0374   -0.3523    5.7016   -0.9538   -0.8648   -1.1807
   94 BN02       2.8899    0.7550    1.2316    0.6042   -0.2166    0.9332
   95 BN03       2.8301    3.1418    1.6085    1.3693   -0.5391    1.9061
   96 BN04       1.2270    1.7783    2.1345    2.2922   -1.6462    2.7948
   97 BN05       2.5499    1.0925    3.0762    0.6970   -0.3102    3.4710
   98 BN06       1.5481   -0.3531    5.7726   -1.1221   -0.9557    1.4061
   99 BN07       2.6561    1.8977    4.1060    1.4792   -0.9293    0.6115
  100 BN08       2.7163    0.3841    4.2278    1.0020   -0.8170    1.8554
  101 BN09       2.4322    0.7865    3.5991    0.7642    0.1361   -1.3757
--------------------------------------------------------------------------------

plots = 101
```

Pearson and Kendall Correlations with Ordination Axes N= 101

Axis:	1			2			3		
	r	r-sq	tau	r	r-sq	tau	r	r-sq	tau
DENSIO	-.907	**.822**	-.718	-.190	.036	-.154	-.050	.002	.019
SOSTEMS	.382	.146	.297	.557	.310	.406	-.153	.024	-.105
QILI IV	-.022	.000	.017	.949	**.902**	.839	.000	.000	.008
OVERSTORY	-.789	.622	-.670	-.274	.075	-.157	-.225	.051	-.106
UNDERSTORY	-.523	.274	-.419	.180	.032	.179	.028	.001	-.006
HISHRUB	-.139	.019	-.096	.776	.602	.605	-.018	.000	.058
LOSHRUB	.199	.040	.171	.275	.075	.048	.276	.076	.262
OSPINRIG	-.390	.152	-.318	-.010	.000	.009	-.240	.057	-.175
OSPINSTR	-.222	.049	-.169	-.338	.114	-.249	-.172	.030	-.115
OSPINRES	-.231	.053	-.177	-.203	.041	-.071	-.149	.022	-.141
OSQUEALB	-.535	.287	-.428	-.224	.050	-.165	.204	.041	.267
OSQUESTE	-.152	.023	-.095	.353	.125	.274	-.206	.043	-.103
OSQUEVEL	-.452	.204	-.382	-.218	.047	-.143	.018	.000	.093
USQUEALB	-.434	.188	-.394	-.163	.027	-.139	.331	.109	.278
USQUESTE	-.331	.109	-.267	.393	.155	.323	-.198	.039	-.179
USQUEVEL	-.329	.108	-.267	-.122	.015	-.100	.386	.149	.271
USQUEILI	-.205	.042	-.153	.311	.097	.254	-.165	.027	-.177
HIQUEALB	-.228	.052	-.157	-.056	.003	-.031	.653	.427	.457
HIQUESTE	-.011	.000	.015	.344	.119	.285	.035	.001	.018
HIQUEVEL	.023	.001	.008	.042	.002	.066	.706	.499	.432
HIQUEILI	-.128	.017	-.041	.865	.748	.757	.155	.024	.036
HIGAYBAC	-.486	.236	-.457	-.187	.035	-.182	.015	.000	.062
LOQUEALB	-.032	.001	-.071	-.078	.006	-.060	.571	.326	.435
LOQUESTE	.495	.245	.413	-.073	.005	-.073	.395	.156	.290
LOQUEILI	.102	.010	.096	.818	.669	.759	-.028	.001	.023
LOQUEPRI	.235	.055	.235	.723	.523	.607	-.206	.043	-.164
LOVACSPP	-.518	.269	-.406	.134	.018	.161	.377	.142	.301
LOGAYBAC	-.671	.450	-.529	.206	.042	.142	.280	.078	.238
LOKALANG	-.040	.002	-.013	.531	.282	.420	-.307	.094	-.284
LOPTEAQU	.329	.108	.254	.363	.132	.288	.462	.213	.377
LOCOMPER	.566	.321	.465	.018	.000	.029	.403	.163	.208
LORUBUS	.528	.279	.414	-.352	.124	-.262	-.075	.006	-.011
LOGRASSEDGE	.655	.429	.507	-.458	.209	-.357	-.106	.011	-.057
LOMOSSLICHEN	.349	.122	.292	.094	.009	.089	.422	.178	.294
LOASTERACEA	.672	.452	.540	-.441	.194	-.338	-.192	.037	-.117

APPENDIX C

Logistic Regression results for all variables having r^2 values > 0.4 on the Pearson and Kendall Correlation Matrix for Axes 1 and 2 of Principle Components Analysis (see Appendix A). Because of correlations between variables, all variables were analyzed individually. Three variables (DENSIO, QILI IV, and OVERSTORY) showed significance for predicting *H. maia* presence at $p \leq 0.05$ (bold).

AXIS 1: DENSIO, OVERSTORY, LOASTERACEA, LOGAYBAC, LOGRASSEDGE

Parameter	df	Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square
Intercept	1	-1.0674	0.4749	5.0509	0.0246
DENSIO	1	-0.0265	0.0116	5.2045	**0.0225**

Parameter	df	Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square
Intercept	1	-1.3374	0.3797	12.4063	0.0004
OVERSTORY	1	-0.0382	0.0178	4.6348	**0.0313**

Parameter	df	Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square
Intercept	1	-1.9722	0.9045	4.7545	0.0292
LOASTERACEA	1	0.0187	0.0258	0.5225	0.4698

Parameter	df	Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square
Intercept	1	-1.8310	0.5760	10.1031	0.0015
LOGAYBAC	1	-0.0251	0.0221	1.2933	0.2554

Parameter	df	Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square
Intercept	1	-2.3180	0.9036	6.5812	0.0103
LOGRASSEDGE	1	0.00638	0.0254	0.0631	0.8016

AXIS 2: QILI IV, HIQUEILI, LOQUEILI, HISHRUB, LOQUEPRI

Parameter	df	Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square
Intercept	1	-3.1333	0.6943	20.3659	<.0001
QILI IV	1	0.2788	0.1433	3.7859	**0.0517**

Parameter	df	Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square
Intercept	1	-2.4718	0.6389	14.9666	0.0001
HIQUEILI	1	0.0133	0.0117	1.2962	0.2549

Parameter	df	Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square
Intercept	1	-2.4775	0.5714	18.7996	<.0001
LOQUEILI	1	0.0239	0.0162	2.1781	0.1400

Parameter	df	Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square
Intercept	1	-2.4043	0.5173	21.6047	<.0001
HISHRUB	1	0.00828	0.0103	0.6488	0.4205

Parameter	df	Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square
Intercept	1	-1.1743	0.4973	5.5765	0.0182
LOQUEPRI	1	-0.00965	0.0344	0.0786	0.7792

APPENDIX D

Description of habitat variables (mean + SE) measured at *H. maia* locations and in nine vegetation types on Martha's Vineyard, MA. Variables displayed are those having r^2 values > 0.4 on the Pearson and Kendall Correlation Matrix for Axes 1 and 2 of Principle Components Analysis (see Appendix A).

VARIABLES FROM AXIS 1

Site Type	DENSIO	OVERSTORY	LOW ASTERACEA	LOW GAYBAC	LOW GRASS-SEDGE
HM	27.00 ± 7.11	9.32 ± 3.52	10.68 ± 6.24	9.09 ± 3.57	7.27 ± 5.69
GR	37.27 ± 7.34	19.75 ± 6.43	11.00 ± 6.13	2.75 ± 1.42	34.75 ± 9.34
OW	75.85 ± 5.24	65.00 ± 5.83	0	50.50 ± 7.41	0
OW/SO	59.45 ± 5.51	39.00 ± 6.47	0	32.25 ± 8.88	0
SO	26.56 ± 8.55	14.25 ± 8.98	0.25 ± 0.25	13.50 ± 5.42	0.25 ± 0.25
YP	74.84 ± 7.64	61.75 ± 10.33	0	24.50 ± 7.67	0.25 ± 0.25
MP	86.24 ± 3.66	53.25 ± 11.41	0	7.50 ± 3.82	0.25 ± 0.25
PP	81.51 ± 3.38	70.25 ± 8.19	0	55.50 ± 10.12	0
HW	9.68 ± 3.83	3.25 ± 1.97	26.25 ± 6.08	1.50 ± 1.50	22.75 ± 4.19
BN	20.11 ± 3.11	1.50 ± 1.50	0.50 ± 0.33	10.00 ± 2.04	2.00 ± 1.48

VARIABLES FROM AXIS 2

Site Type	QILI IV	HIGH QUEILI	LOW QUEILI	HIGH SHRUB	LOW QUEPRI
HM	4.45 ± 0.72	38.41 ± 10.85	30.45 ± 6.66	40.45 ± 10.60	7.50 ± 3.40
GR	1.30 ± 0.40	6.00 ± 3.79	4.50 ± 1.78	11.25 ± 3.75	0.50 ± 0.33
OW	3.40 + 0.31	22.00 ± 5.02	18.25 ± 3.44	24.25 ± 5.18	0
OW/SO	5.80 ± 0.33	60.25 ± 7.70	35.75 ± 5.52	65.00 ± 5.83	3.75 ± 1.91
SO	5.40 ± 0.56	52.75 ± 11.05	37.00 ± 6.76	60.00 ± 10.67	20.00 ± 5.07
YP	2.90 ± 0.84	27.00 ± 10.45	14.50 ± 5.35	43.25 ± 11.27	3.50 ± 1.94
MP	0.60 ± 0.31	1.75 ± 1.49	0.75 ± 0.38	16.50 ± 4.93	0
PP	2.40 ± 0.69	20.00 ± 9.57	10.50 ± 3.69	31.75 ± 10.69	1.75 ± 1.49
HW	0.90 ± 0.31	3.25 ± 1.97	2.75 ± 1.42	9.50 ± 3.67	0.75 ± 0.38
BN	6.70 ± 3.11	22.75 ± 4.19	26.25 ± 6.08	33.25 ± 4.67	3.00 ± 1.38

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