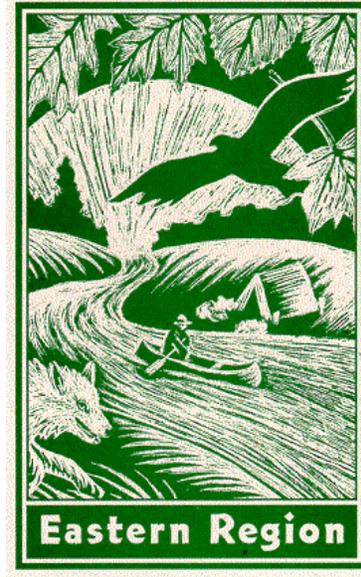


Conservation Assessment
for the
West Virginia White (*Pieris virginiensis* Edwards)



USDA Forest Service, Eastern Region
February 4, 2005

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This document is undergoing peer review, comments welcome

This Conservation Assessment was prepared to compile the published and unpublished information on the subject taxon or community; or this document was prepared by another organization and provides information to serve as a Conservation Assessment for the Eastern Region of the Forest Service. It does not represent a management decision by the U.S. Forest Service. Though the best scientific information available was used and subject experts were consulted in preparation of this document, it is expected that new information will arise. In the spirit of continuous learning and adaptive management, if you have information that will assist in conserving the subject taxon, please contact the Eastern Region of the Forest Service - Threatened and Endangered Species Program at 310 Wisconsin Avenue, Suite 580 Milwaukee, Wisconsin 53203.

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EXECUTIVE SUMMARY

The West Virginia white butterfly (*Pieris virginiensis*) was first described by Henry Edwards in 1870 as a subspecies of the holarctic mustard white butterfly (*Pieris napi* L.) (see Edwards, 1872). In 1964, *P. virginiensis* was given full species status, supported by behavioral, biochemical and biological differences between the two taxa. *Pieris virginiensis* is conspecific with the mustard white in the northern portions of its range (Upper Midwest and Northeast; southern Canada). However, the two segregate into distinct habitat types: the West Virginia white occurring only in mesic Maple-beech-birch Forests and the mustard white inhabiting Canadian Zone forests, parklands and wetlands.

Historically, *Pieris virginiensis* was known to occur from Vermont west to Wisconsin and southeast (primarily in the Appalachian Mountains) to extreme northeast Alabama. The habitat for this butterfly is mature, mesic hardwood forests, typically dominated by basswood, beech, birch and/or maple, with a minimum of subcanopy or underbrush. The larvae feed primarily on the toothworts *Dentaria diphylla* and *Dentaria heterophylla*, occasionally using cut-leaved toothwort (*Dentaria laciniata*) and rock mustard (*Arabis laevigata*). Habitat descriptions for the primary larval foodplants also correlate them with mature, mesic forests and the butterfly rarely ventures from dense forest into treeless habitats. The West Virginia White is single-brooded, with adults appearing only once from April through early June. Upon hatching from their eggs, the larvae must feed and mature rapidly, prior to senescence of the foodplants in July.

Because of its restriction to mature, undisturbed forests, the ephemeral nature of its life cycle and limited foodplant tolerance, the West Virginia White is sensitive to the deleterious effects of habitat fragmentation, altered succession cycles and invasion by alien species. In particular, the invasion of mesic forests by introduced Garlic Mustard (*Alliaria petiolata*) was noted as posing an imminent threat to the long-term survival of this species throughout much of its historic range. The application of pesticides to mixed hardwood forests, aimed at controlling outbreaks of the introduced Gypsy moth (*Lymantria dispar* L.), was also thought to have played a part in these observed reductions in population size and distribution.

In the late 1990's and early 2000's, a heightened effort to survey for viable *Pieris virginiensis* populations was undertaken throughout its known range. These surveys suggest that the species is continuing to lose habitat and populations in many states where it was once common, particularly the Northeast. However, certain Federal and State owned forests continue to support what appear to be large populations of this species, despite habitat that is often highly fragmented. This continued decline across much of its historic range is attributed to many factors and has led to the production of the following Conservation Assessment.

ACKNOWLEDGEMENTS

I would like to thank Steve Olson (previously Botanist with the Hoosier National Forest) for providing information on the distribution of *Dentaria* species within the Hoosier NF. Mr. Olson also directed me to the first verified record of *Pieris virginiensis* from the Forest (Charles C. Deam Wilderness). Kelle Reynolds (also previously with the Hoosier NF) was instrumental in

organizing funding and support documentation to make this Conservation Assessment possible. Kirk Larson (current Botanist with the Hoosier NF) has also provided much needed support from the Forest. Finally, I would like to thank Dr.'s Edward Voss (Professor Emeritus at the University of Michigan) and Dr. Warren H. Wagner Jr. (now deceased, former Professor Emeritus at U of M), for introducing me to the West Virginia white butterfly many years ago.

NOMENCLATURE AND TAXONOMY

The West Virginia White Butterfly (*Pieris virginiensis* Edwards) is a member of the butterfly family Pieridae, which contains about 1,100 species worldwide and 58 in North America (Scott, 1986). Many Pieridae are either white or yellow and are often called "whites" and "sulfurs". The white pigment in their wings advertise that these butterflies are distasteful because of the mustard oils they retain from their foodplants (Scott, 1986). A common representative of this widespread family is the ubiquitous garden pest, the introduced Cabbage Butterfly (*Pieris rapae* L.).

Pieris virginiensis was first described by Henry Edwards, from specimens collected at Kenawha, West Virginia (Edwards, 1872; Hovanitz, 1963; Klotz, 1954). Edwards, and many others at the time, considered this butterfly a subspecies of the circumboreal mustard white, *Pieris napi* L. In 1963, *P. virginiensis* was given full species status by Hovanitz, who went on to discuss the physical feature separating it from the North American representative of the mustard white, *Pieris napi oleracea* Edwards (now considered itself a distinct species, *P. oleracea* Edw.). This determination has been further supported by observed behavioral, biochemical and biological differences between the two taxa (see Bowden, 1971; Chew 1980, 1981). Some (mainly European) authors place *P. virginiensis*, *P. oleracea* and *P. rapae* in a separate genus, *Artogeia* Verity.

The primary larval foodplants, toothworts (*Dentaria* spp.), have also undergone some recent taxonomic revision and are currently placed in the genus *Cardamine* (see Biota of North America Program, 1998). *Dentaria diphylla* is now *Cardamine diphylla*, while *Dentaria heterophylla* is *Cardamine angustata* and *D. laciniata* is *Cardamine concatenata*. For the purposes of continuity with the more recent literature on the butterfly, I have retained the earlier names, based on *Dentaria*.

DESCRIPTION OF SPECIES

ADULT DESCRIPTION

The West Virginia White is a relatively small butterfly, measuring approximately 1.5 inches (3.5cm) in wingspan. The wings are dusky white, somewhat translucent, with a minimum of dark markings on the upper surface (see Figures 1-2; also Hovanitz, 1963; Howe, 1978; Klotz, 1951; Opler, 2004; Opler and Krizek, 1984; Opler and Malikul, 1992; Scott, 1986; Voss and Wagner, 1956). These dorsal markings are usually reduced to a thin outer margin of dark, ash gray to brown gray scales on the forewings, a darkened apical tip on the forewings, and a slight darkening of the veins on the hindwings. The female is often more heavily marked than the male

and may have a pair of faint, round brown gray spots in the outer area of the forewings, as depicted in Hovanitz (1963) and reproduced here as Figure 1. On the undersurface, the veins of the hindwings are outlined with fuscous gray scales (see Figure 2). Often the veins at the terminal area of the ventral forewings and the base are also darkened with ash-gray scales.

Adults are distinguished from the spring brood of the closely related *Pieris oleracea* by its near total lack of yellow coloration to the ventral (under) wing surfaces and a general suffusion of the dark markings. Typically, the West Virginia white has a small, egg-yolk yellow spot or crescent at the upper edge of the base of the ventral hindwing. When the two species are compared, *Pieris oleracea* appears to have heavier scaling on its wings (both light and dark) making them more opaque and bright white; the dark markings are crisp in outline and dark brownish-black in coloration (see Figures 1 and 2). The ventral surfaces of both the hindwings and terminal area of forewings are always washed with lemon yellow, even in the relatively unmarked summer broods (see figure 2, upper right individual).

Pieris virginiensis does not produce a summer brood under normal conditions, although occasional summer individuals do emerge under laboratory conditions (Bess, 2004; Courant and Chew, 1995; Shapiro, 1971). These late season individuals are sometimes darker in color on the dorsal surface, but lack dark scaling on the undersurface veins. If these second brood individuals occur in the wild, they are not believed to produce viable progeny, given the lack of larval foodplants at the time of flight.

DESCRIPTION OF IMMATURE STAGES

The eggs of *Pieris virginiensis* are small (~0.003 inches in diameter), white and spherically conical in shape. Upon high magnification, the surface of the egg is sculpted into a latticework of tiny pits and projections (see Scott, 1986 - Figure 45 and Color Plate 1). They are laid singly on the foodplant and the larvae hatch in a few days. The young caterpillars are yellowish green, becoming a dull grass green with maturity. The skin surface is covered with a short, dense layer of hairs, making the caterpillar feel fuzzy to the touch and giving it a whitish or "silvered" appearance in light. There are also scattered, somewhat longer hairs, translucent or whitish in color, all over the body. Narrow, indistinct dorsal and lateral lines are yellow-green. The caterpillars blend in very well with the leaves on which they feed. Pupation occurs on either the foodplant or adjacent vegetation, typically within one foot of the ground surface. The pupa is angular, with a frontal projection that distinguishes it from all other North American *Pieris* (see Klots, 1954). The pupa is typically green to brownish and attached to a plant stem with silk at both the terminal end and a loop around the middle.

LIFE HISTORY

REPRODUCTION

Like all other Lepidoptera, the West Virginia White is a holometabolus insect, meaning it passes through four distinct life stages: egg, larva, pupa and adult. The species is single brooded, with the adults appearing from mid-April through early June (depending on latitude and altitude). The adults are fairly short lived, with individuals typically surviving 5-10 days. They mate quickly upon emergence from the pupa and females lay eggs (oviposit) on the leaves of the larval

food plants, usually native mustards of the genus *Dentaria*. The brief egg stage (5-10 days) is followed by a relatively short larval stage (5 instars; 10-20 days), and an extended pupa stage (10-11 months in most cases). While many butterflies tend to mate in the morning, Forsburg and Wiklund (1989) found the closely related *Pieris napi* also mates in the afternoon and that females mated with multiple males.

ECOLOGY

Overview

West Virginia white butterflies occur only in mature hardwood forest and mixed hardwood-conifer forest remnants. The adult brood emerges in the spring prior to full canopy leaf out, which coincides with flowering time of the larval foodplants. Eggs are laid directly on the foodplant(s). The larvae hatch and develop quickly, feeding on toothworts (*Dentaria diphylla*, *D. heterophylla* and sometimes *D. laciniata*) and rock cress (*Arabis laevigata*) which grow in these habitats (Calhoun and Iftner, 1988; Hovanitz, 1963; Klots, 1935, 1954; Opler, 2004; Shuey and Peacock, 1989; Schweitzer, 2004; Opler 2002; Voss and Wagner, Wagner, 1956). The foodplants, particularly *Dentaria*, senesce early and are usually completely withered by late June. Therefore, the life cycle of the West Virginia White butterfly correlates closely with the ephemeral life cycle of the foodplant(s); a short adult and egg stage, rapid growth during the larval stage, followed by long-term hibernation/aestivation as a pupa.

Adult Ecology

Adults of the species take flight once per year, generally during late May and early June in the northern portion of its range, see Wagner (1978) and Wagner and Voss (1956). The southern populations fly from April to early May, depending on altitude (Harris, 1972; Hovanitz, 1964; Mather, 1963; Opler, 2004). Newly emerged adult males often search for females along streams or damp areas near woodland roads (Opler and Krizek 1984). Females often mate within a few hours of emerging, and some Pieridae are known to mate with multiple partners over the course of their flight period. Forsberg and Wiklund (1989) discuss the selective advantages of afternoon mating in the closely related *Pieris napi*.

West Virginia White Butterflies consume nectar from host plant flowers and others, such as white wake-robin (*Trillium*), Canada violet (*Viola canadensis* and other *Viola* spp.), spring beauty (*Claytonia virginica*), and garlic mustard (Opler and Krizek 1984, Opler 2002). Indiana populations were observed mating on and nectaring at *Dentaria heterophylla* and *D. laciniata*, with additional nectar sources including trout lily (*Erythronium*), wild geranium (*Geranium maculatum*), Virginia bluebells (*Mertensia virginica*), woodland phlox (*Phlox divaricata*) and garlic mustard (*Alliaria petiolata*) (see Bess, 2004; Opler, 2004; Yahner, 1998).

Adults tend to fly close to the ground with a slow, but determined pace, becoming rapid flyers capable of escaping into the canopy when alarmed. Opler and Krizek (1984) state that newly emerged adult males tend to occur along streams or damp areas near woodland roads. The adults frequently rest on herbaceous vegetation to sun themselves, particularly the females. They also rest on herbaceous vegetation, often under shrubs (Harris, 1972), during times of inactivity. Females lay eggs singly on the undersides of the leaves of the host plant (Opler 2002). In an Ohio study, females oviposited more on plants on a southeast-facing slope, possibly because of prolonged insolation that enhances development of larvae (Shuey and Peacock 1989). The eggs

take from 5 to 10 days to mature, upon which the young larvae emerge and begin feeding on the host plant.

Larval Ecology

The caterpillar of *Pieris virginiensis* was long thought to feed exclusively on toothworts, particularly *Dentaria diphylla* and *D. heterophylla* (Calhoun and Iftner, 1988; Hovanitz, 1963; Klots, 1935, 1954; Wagner, 1978). Most early reports refer only to *D. diphylla*. In Ohio, Calhoun and Iftner (1988) found that *Pieris virginiensis* females selected *Dentaria heterophylla* (reported as *D. multifida*) for oviposition. In central and southern Indiana, females were repeatedly observed ovipositing on *Dentaria heterophylla* growing in mesic, riparian maple-beech-birch forests (Bess, 2004). The related *Dentaria laciniata* has often been reported as a potential foodplant for *P. virginiensis*, however, little evidence of its use exists (Cappuccino and Kareiva, 1985; Simpson, 1993). For example, Cappuccino and Kareiva (1985) found that very few eggs were laid on *D. laciniata* compared to *D. diphylla*. Although larval growth was normal on *D. laciniata*, fewer larvae survived on it because it senesced much earlier than *D. diphylla*. *Dentaria laciniata* also occurs in drier, sandier and more degraded habitats than other *Dentaria* species or the West Virginia White appear able to withstand.

Recent research has shown that other mustard species are also used as food by *Pieris virginiensis* larvae (Calhoun and Iftner, 1988; Cappuccino and Kareiva, 1985; Shuey and Peacock, 1989; Simpson, 1993). Shuey and Peacock (1989) identified *Arabis laevigata* as an additional host where *D. diphylla* was not present. They found that butterfly selection of *Arabis laevigata* was significantly more frequent than *D. laciniata* for ovipositing, likely because *A. laevigata* is not a short-lived ephemeral (Bloom et al., 1990; Shuey and Peacock 1989). It may also be producing more or better oviposition stimulants than *D. laciniata*. The researchers did not mention *D. heterophylla*.

Cappuccino and Kareiva found that the young larvae (instars I-III) stay on the undersides of leaves and older larvae (instars IV and V) stay mainly on the tops of them. Young larvae also hide in the inflorescence and developing leaves, while feeding on these tender parts (Bess, 2004). The fully mature larvae consume flower pods in their entirety and can act as leaf scrapers, removing the lower dermis and mesophyll of the leaf, while leaving the transparent surface cuticle. Typically, young larvae feeding on the young and developing plant parts, older larvae exploiting the fully mature leaves and fruit. However, asynchronous events that lead to early plant senescence require caterpillars to find additional plants (Cappuccino and Kareiva 1985).

Under lab conditions of constant light and warm temperatures, these butterflies have emerged from pupae during the same season and produced a second brood (Bess, 2004; Courant and Chew, 1995; Shapiro 1971). Only vague details exist about naturally occurring, 2-brooded populations in the Northeast (see Courant and Chew 1995). There is no evidence that West Virginia whites can remain in the pupal stage for 2 years or more, as can some other Pieridae (Cappuccino and Kareiva 1985).

DISPERSAL/MIGRATION

The West Virginia White is not known to migrate and does not typically fly outside the confines of closed canopy forest (Cappuccino and Kareiva, 1985; Klots, 1951; NatureServe, 2004; Opler,

2004). Large open areas without trees are indicated in the literature as being impediments to the dispersal of this species. These include old fields, utility right-of-ways and roads. Therefore, when this species has been eradicated from a site, the ability of nearby colonies to re-populate the area is constrained by the degree of forest fragmentation.

OBLIGATE ASSOCIATIONS

West Virginia White butterflies require areas of mature, maple-beech-birch forest that contain large populations (hundreds or thousands of individuals) of the larval foodplants. The West Virginia White is apparently monophagous on *D. diphylla* in the northern part of its range, because it is often the only acceptable mustard species present. Although *D. laciniata* often co-occurs with this species, it does not appear to be a preferred foodplant of the butterfly. Typically the West Virginia white is not found in forests only containing *D. laciniata*. *Dentaria diphylla* also has a longer phenology (senesces later) than *D. laciniata*, allowing more time for larvae to complete their development (Shuey and Peacock 1989). Adult nectar sources are also necessary for this species, and the larval foodplants and other herbaceous species typical of mature beech maple forests are utilized (see Yahner, 1998).

In the central and southern parts of its range, the West Virginia White uses the closely related *Dentaria heterophylla* as a foodplant. Some local populations of the butterfly are also utilizing *D. laciniata* (see Simpson, 1993) and other mustards such as *Arabis laevigata* for larval development. In Ohio, Shuey and Peacock (1989) identified *Arabis laevigata* as an additional host. In their studies, larvae also readily consumed and developed on the foliage of this species. However, within the landscape covered by *Pieris virginiensis*, *Dentaria heterophylla* is by far the most commonly encountered native mustard occurring in mature, mesic maple-beech-birch forests. In Indiana, this butterfly has not been observed in association with *Dentaria laciniata* in the absence of other *Dentaria* spp. (Bess, 2004).

HABITAT

RANGE-WIDE

Pieris virginiensis occurs only in mature, mesic deciduous forest and northern pine-hardwood forests (Hovanitz, 1963; Klotz, 1954; Nielsen, 1999; Opler and Krizek, 1984; Opler and Malikul, 1992; Opler, 2004; Pyle, 1981; Schweitzer, 2004), including northern hardwood forests and hardwood swamps (NatureServe 2004), where hostplants are abundant (Glassberg 1999). In Ohio and parts of Michigan, this species survives in scattered sugar maple (*Acer saccharum*) and beech (*Fagus grandiflora*) woodlots within a landscape of rolling farmland (Bess, 2004; Shuey and Peacock 1989). The primary tree species in a Connecticut habitat were sugar maple and beech, with several oak and hickory (*Carya*) species also abundant (Cappuccino and Kareiva 1985). A population in Massachusetts used a woodland of beech, maple, and hemlock (Courant and Chew 1995). In northern Michigan, the butterflies occur primarily in forests dominated by sugar maple and basswood, with varying amounts of beech (Bess, 2004; Voss and Wagner, 1956; Wagner 1978).

Typically the canopy is dominated by beech and maple, with Yellow Buckeye (*Aesculus flava*), Birches (*Betula alleghaniensis*, *B. papyrifera*), Hickories (*Carya* spp.), White Ash (*Fraxinus*

americanus), Tuliptree (*Liriodendron tulipifera*), Sycamore (*Platanus occidentalis*), Black Cherry (*Prunus serotina*), White Oak (*Quercus alba*), Red Oak (*Quercus rubra*) and Basswood being locally or regionally important. In the north and at higher elevations, White Pine (*Pinus strobus*) and/or Hemlock (*Tsuga* spp.) may also be present. In the south, Magnolias (especially *Magnolia acuminata* and *M. fraseri*) are important components of the canopy and subcanopy. The formerly dominant American chestnut (*Castanea dentata*) is still represented in these southern forests by thickets of stump sprouts and occasionally young trees.

In older representatives, shrub and subcanopy layers tend to be sparse, with scattered individuals of young conifers, canopy hardwoods and other shade tolerant species. This lack of subcanopy and shrub layers is often a sign of past grazing, which removes particular age classes, based on when the grazing occurred in the history of the forest. True shrubs include moosewood (*Acer pennsylvanicum*), mountain maple (*A. spicatum*), shadbush (*Amelanchier* spp.), blue beech (*Carpinus carolinus*), witch hazel (*Hamamelis virginiana*), spicebush (*Lindera benzoin*), hornbeam (*Ostrya virginiana*), blackberries (*Rubus* spp.), elderberry (*Sambucus*), blueberries (*Vaccinium pallidum* and others), and viburnums. In the southern mountains, azaleas, rhododendrons and mountain laurel (*Kalmia latifolia*) can also be locally important. Vines such as wild grape (*Vitis* spp.) and Virginia creeper (*Parthenocissus*) are often common, particularly on grazed sites.

The herbaceous layer in undisturbed examples of these forest types is species rich and includes numerous ferns (such as *Asplenium*, *Athyrium*, *Botrychium*, *Dryopteris*, *Lycopodium*, *Polystichum* and *Thelypteris*), grasses, sedges and wildflowers. Grasses and sedges tend to be scattered and clump forming, although sometimes composing the dominant ground cover. Typical species are; *Brachyeletrum erectum*, *Carex albursina*, *C. careyana*, *C. intumescens*, *C. laxiflora*, *C. pennsylvanicum*, *C. plantaginea*, *C. platyphylla*, *Cinna arundinacea*, *Danthonia spicata*, *Elymus hystrix*, *Panicum commutatum ashei*, *P. latifolium*, *Poa alsodes* and many others.

Representative wildflowers include; baneberries (*Actaea pachypoda*, *A. rubra*), wild ramps (*Allium* spp.), rue anemone (*Anemone cinquefolia*), jack-in-the-pulpit (*Arisaema triphyllum*), Canada ginger (*Asarum canadense*), *Aster* spp.), blue cohosh (*Caulophyllum thalictroides*), spring beauty (*Claytonia virginica*), toothworts (*Dentaria* spp.), dutchman's breeches (*Dicentra cucullaria*), trout lily (*Erythronium americanum*), wild licorice (*Galium circaezans*), wild geranium (*Geranium maculatum*), Canada mayflower (*Maianthemum canadense*), Virginia bluebells (*Mertensia virginica*), mitrewort (*Mitella diphylla*), partridge berry (*Mitchella repens*), sweet cicely (*Ozmorhiza claytoni*), ginseng (*Panax quinquefolius* and *P. trifolius*), *Phacelia* spp., woodland phlox (*Phlox divaricatus*), mayapple (*Podophyllum peltatum*), Jacob's ladder (*Polemonium reptans*), Solomon's seal (*Polygonatum pubescens*), *Pyrola* spp., goldenrods (*Solidago* spp.), trilliums (*Trillium* spp.), violets (*Viola* spp.) and a variety of orchids.

NATIONAL FORESTS

Chequamegon-Nicolet National Forest

The Chequamegon-Nicolet populations of the West Virginia White occur in Maple-Basswood-Birch forests with a herbaceous flora containing the northern component of those listed above. The Wisconsin populations are thought to feed exclusively on *Dentaria diphylla*, and possibly *D.*

laciniata to a lesser extent. The butterfly occurs primarily within the Nicolet NF (numerous occurrences, 14 recent), with only a single population within the more western Chequamegon NF boundary (see USDA 2004a).

Hoosier National Forest

The *Pieris virginiensis* populations on the Hoosier NF occur in middle-aged (60-80 years old) and mature (>150 years old) hardwood forests on mesic lower slopes; typically on old alluvial terraces along major streams and small rivers. These forests are dominated by sugar maple, beech, tuliptree white ash, white oak, red oak and basswood (see Bess, 2004). Yellow birch (*Betula alleghaniensis*), sycamore and black cherry are locally important. The shrub layer is composed primarily of young sugar maples, with scattered witch hazel and numerous spicebush. *Dentaria heterophylla* forms clonal patches throughout these forests and is the primary foodplant in Indiana. *Dentaria laciniata* is also locally common, co-occurring with *D. heterophylla*. *Dentaria diphylla* occurs in far fewer locations, although it is likely used where the butterfly and plant co-occur.

SITE SPECIFIC

Other than the descriptions given above, specific information is not available on the composition of habitat in butterfly occupied sites within the two forests at this time.

DISTRIBUTION AND ABUNDANCE

The USDA Natural Resource and Conservation Service (NRCS) maintains maps on the distribution of remaining U. S. forest types at its national Website: <http://plants.usda.gov>. For the purposes of this report, maps of current (1992), non-federal holdings in the beech-birch-maple complex of forest types (see Figure 3) were selected as the base map for plotting known locations of *Pieris virginiensis* and its two primary foodplants, *Dentaria diphylla* and *D. heterophylla* (Figures 3 and 4, respectively). *Dentaria* records came from a variety of sources including Cooperidge et al. (2002), Deam (1946), Easterly (1964), Long (1956), Montgomery (1955, 1957), USDA: NRCS (2004) and Voss (1972).

HISTORIC (1800) DISTRIBUTION

The distribution of the West Virginia White Butterfly has always been tied closely with that of its obligate habitat; mature, mesic hardwood forests. Historically, these forests were concentrated in southern Ontario and Quebec, the Great Lakes states and from New England, south along the Appalachians to North Georgia and extreme northeast Alabama (see Eyer, 1980; Hutchinson, 1996; Kuchler, 1964; Leverett, 2000). The large-scale deforestation that occurred throughout the range of this species between 1830 and 1950, resulted in region-wide fragmentation of the eastern hardwood forests (Foster and O'Keefe, 2000; Hutchinson, 1996; Leverett, 2000; Louckes et al.). This likely had a profound effect on the butterfly by reducing metapopulation size and restricting gene flow between what are now often highly isolated subpopulations.

Figure 3 gives a hypothetical historic (ca. 1800) distribution for the West Virginia White based on known records of the butterfly (see Hovanitz, 1963; Layberry et al., 1998; Opler, 2004), the historic distribution of maple-beech-birch-birch forests and the distribution of *Dentaria diphylla*

and *D. heterophylla*. *Dentaria laciniata* has a much broader range of known habitats than either plant species or the butterfly and is here considered a minor foodplant. The distribution of the primary larval foodplants, large expanses of unbroken forest cover and cool summer temperatures were likely the key factors regulating the historic distribution of the West Virginia White.

RECENT DISTRIBUTION (1900-2004)

To date, the West Virginia white has been reported from 19 States and two Canadian Provinces (see Figure 4). Prior to its discovery in Georgia in 1961, the southward range was believed to end in North Carolina and Tennessee (Hovanitz, 1963). Shortly thereafter, the species was found across the border in northeastern Alabama, making these the southernmost records to date. If Figure 3 is taken as the maximum potential distribution for *Pieris virginiensis* at the time of westward expansion by original European colonists (~1800), then the current distribution (Figure 4) covers approximately one-fourth of the potential range for this species.

As reported in the literature, populations of the West Virginia White tend to be rare, local and widely scattered. They are always closely associated tracts of contiguous maple-beech-birch-birch forest. It is acknowledged that many of the historic populations shown in Figure 4 have been extirpated. Despite the large-scale reduction in the distribution of mature hardwood forests, the West Virginia White is still considered locally common by Lepidopterists in the southern and mid-Appalachians (Glassberg 1999). Through a renewed survey effort, additional populations are being discovered in several states, although the species continues to decline in others.

The distribution of the West Virginia White through the Ohio Valley is currently becoming better understood. Opler's (2004) distribution map shows confirmed records in Kentucky, just across the Ohio River from both the southern tip of Illinois and south-central Indiana. However, Pyle and Malikul (1992) showed the range extending from northern Kentucky into southern Indiana, but not Illinois. Porter (1994) reports the species from Marion Co. in south-central Indiana, and Eiler found it in extreme southern Indiana. Recent surveys in central Indiana have located large populations in the Charles Deam Wilderness Area of the Hoosier NF, which is comprised almost entirely of potential habitat for this butterfly (Bess, 2004). Historic records for 5 populations are known from similar habitat in the southern third of the state (see Eiler, 1987a-b), at least 4 of which are still extant (Bess, 2004). An isolated population occurs near the Michigan state line and several others could occur nearby. There are no verified records for *Dentaria diphylla*, *D. heterophylla* or *Pieris virginiensis* from Illinois, although literature records report *D. heterophylla* from "Illinois" (see Britton and Brown, 1913).

STATE AND NATIONAL FOREST DISTRIBUTION

State Forest (SF), State Reservation (SR), State Park (SP), State Fish and Wildlife Area (SFWA), State Wildlife Management Area (SWMA), National Forest (NF), National Lakeshore (NL) and National Monument (NM) lands within the range of the West Virginia White and known to contain potential habitat and/or butterflies(*) include:

1. **Alabama** - None. Russell Cave NM possible.
2. **Connecticut** - None, though numerous State Parks.
3. **Georgia** - Chattahoochee NF*.

4. **Indiana** - Hoosier NF*; Clark State Forest*; Crosley SFWA*; Harrison-Crawford SF*; Jackson-Washington SF*; Morgan-Monroe SF*
5. **Kentucky** - Daniel Boone NF*
6. **Maryland** - Dans Mountain WMA; Green Ridge SF; Potomac SF; Savage River SF; South Mt. SP; Swallow Falls SP; Warrior Mt. WMA
7. **Massachusetts** - Beartown SF; Chester-Blandford SF; Daughters American Revolution SF; Federated Women's Club SF; Freetown-Fall River SF; Granville SF; Ken Dubuque SF; Leominster SF; Mohawk Trail SF; Monroe SF; Mt. Everett SR; Mt. Greylock SR; Mt. Tom SR; Mt. Washington SF; October Mt. SF; Otter River SF; Pittsfield SF; Tolland SF; Wachusett Mt. SR.
8. **Michigan** - Hiawatha NF*, Ottawa NF*; Sleeping Bear Dunes NL; Huron-Manistee NF*; Au Sable SF*; Copper Country SF*, Escanaba River SF*; Flat River SGA; Lake Superior SF*; Mackinaw SF*; Pictured Rocks NL; Pierre Marquette SF*; Porcupine Mts SP*; Tahquamenon Falls SP*; Warren Dunes SP; Warren Woods SP.
9. **New York** - Finger Lakes NF; Adirondack Park*; Catskill Park* and numerous SF's.
10. **New Jersey** - Extirpated, Historic.
11. **North Carolina** - Great Smoky Mts NP*; Nantahala NF*; Pisgah NF*; num. SP's
12. **Ohio** - Wayne NF*; Beaver Creek SF; Fernwood SF; Harrison SF; Mohican-Memorial SF; Yellow Creek SF. Numerous State Parks in region.
13. **Pennsylvania** - Allegheny NF*; Cornplanter SF; Delaware SF; Elk SF; Forbes SF, Gallitzin SF; Kittanning SF; Lackawanna SF; Moshannon SF; Sproul SF; Susquehannock SF; Tiadaghton SF; Tioga SF; Wyoming SF; Weiser SF.
14. **South Carolina** - Pisgah NF* and several State Parks within limited region of state where butterfly occurs.
15. **Tennessee** - Cherokee NF; Cumberland Gap NP; Great Smoky Mts NP*; Bledsoe SF*; Lone Mt SF; Morgan SF; Scott SF; Standing Stone SF and numerous State Parks with potential habitat.
16. **Vermont** - Green Mt. NF*; Groton SF; numerous State Parks.
17. **Virginia** - Jefferson NF*; George Washington NF*; Mt. Rogers NRA; Shenandoah NP* and numerous State Parks with potential habitat.
18. **West Virginia** - Monongahela NF*; George Washington NF*; Cabwaylingo SF*; Calvin Price SF*; Coopers Rock SF*; Greenbrier SF; Kanawha SF* (type locality); Kumbrabow SF (Rich Mt.)*; Seneca SF* and numerous State Parks.
19. **Wisconsin** - Nicolet NF and several State Parks within potential range.

While Illinois, New Hampshire, Maine and Minnesota contain superficially appropriate habitat for the West Virginia White, the butterfly has not been recorded from these states. There are no records of *Dentaria diphylla* or *D. heterophylla* from Illinois (Illinois Plant Information Network, 2004) and only *Dentaria laciniata* in the most recent Minnesota flora (Cholewa, 2004). However, Britton and Brown (1913) state that *D. diphylla* occurs "west to Minnesota", indicating the species may no longer occur there.

RANGE WIDE STATUS

Rangewide Status of Habitat

By the late 1800's, logging had cleared nearly 80 percent of the ancient forests that once carpeted much of New England. By 1900, the forests of the northeast were reduced to a mere fraction of their former state and soon, events would change their character forever. Clear cutting forests, while leaving the slash and other "waste", was common practice from "the Berkshires in Massachusetts to the Canadian border" (Leverett, 2001). In 1903 massive wildfires swept through the region, fueled by poor forest management and the incredible amount of slash and waste wood left behind by timber operations. It was this series of catastrophic events that led to the creation of the U. S. Forest Service in 1904. Similar scenarios played out in the Midwest and Southeast.

This widespread, unregulated logging left a high fragmented forest. Subsequent clearing for agriculture has left small (40-200 acre), island woodlots surrounded by a sea of habitat unsuitable for the West Virginia white or its foodplants. Many of the remnant forests left behind little resemble their former state in composition of either the canopy or herbaceous layers. Only in the Upper Peninsula of Michigan, the Adirondacks of New York, Allegheny Mts of Pennsylvania, and the central and southern Appalachians, do large, relatively unbroken tracts of this forest type still occur. A study by Mary Davis (1993) reported only 1,700,000 acres of the remaining forests meet the standards for classification as "old-growth" in the entire eastern United States.

Logging and urban sprawl continue to threaten populations of the West Virginia white, particularly in the northern parts of its range (NatureServe 2004; Pyle 1981). Central and southern Appalachian populations are still considered common by Lepidopterists, although they are often intensely local and highly isolated from one another. They are also isolated from the bulk of the remaining populations to the northwest. Schweitzer (NatureServe 2004) states that the species has been extirpated in New Jersey and is imperiled in Pennsylvania, New York and Connecticut. However, the species is not formally protected in any of these states, at this time. Although it currently appears to be somewhat secure in the Midwest (with several extant populations), both Indiana and Wisconsin have listed this butterfly as a species of concern and begun tracking its long-term population trends.

Rangewide Status of *Pieris virginiensis*

Currently (as of November, 2004), Federal and State Status for the West Virginia White is as follows:

TNC Global Rank: G3

National Rank: N3

State Status: Alabama (SNR), Connecticut (S4), Georgia (SNR), Illinois (SNR), Indiana (S3), Kentucky (S4), Maryland (S3), Massachusetts (S3S4), Michigan (SNR), New Jersey (SH), New York (SNR), North Carolina (S4), Ohio (S3?), Pennsylvania (S2S3), South Carolina (SNR), Tennessee (S3S4), Vermont (SNR), West Virginia (S3S4), Wisconsin (S3) (NatureServe 2004).

Populations in Alabama, Georgia and South Carolina are few and highly isolated, making the species a strong candidate for ranking as S1 or S2 in these states. Only in Connecticut, Kentucky and possibly Michigan is this species considered secure.

POPULATION BIOLOGY AND VIABILITY

Today, the West Virginia White exists as a collection of isolated subpopulations varying greatly in size. In northern Michigan and portions of the Appalachians, there is sufficient inter-connected habitat to allow the formation of "regional metapopulations". However, the bulk of the remaining populations occur on smaller forested tracts surrounded by row crops, old fields and large-scale human development. These habitats are essentially hostile to the butterfly and have been shown to be an impediment to its dispersal. Fortunately, many populations occur on state or federally owned forests, affording them some degree of protection from human development. However, Figure 3 clearly shows that the bulk of remaining maple-beech-birch-birch forests in eastern North America are on non-Federal Lands. Populations on Federal and State Forests are also subject to logging, although currently not at the pace of past centuries.

POTENTIAL THREATS

The primary threats facing the West Virginia White center around loss of habitat, primarily through logging and clearing for agriculture or residential development. In large tracts of similar forest types, small forest clearing and selective thinning operations likely have little negative effect on this species and may even (in some cases) enhance habitat. However, the large-scale forest clearing that occurred over the past 150 years across the eastern U.S., has greatly reduced the amount of available habitat for this and other species requiring large tracts of mature, mesic hardwood forests.

Given the dependence of the West Virginia white on mature maple-beech-birch forest for its continued survival, it has likely experienced a catastrophic reduction in population size over the past 200 years as a result of habitat loss. Anecdotal and written evidence also suggests that *Pieris virginiensis* refrains from flying in open areas, or those with less than 50 percent canopy cover. Cappucino and Kareiva (1985) note that adults in Connecticut were detected up to 1 km from their original capture location within a forested landscape. However, they also noted that the butterflies do not usually disperse across open fields. Powerlines and unshaded roads are also avoided (NatureServe 2004). These factors tend to isolate *Pieris virginiensis* populations from one another in islands of forest, surrounded by essentially hostile habitat. This isolation, coupled with an increase in the relative amount of edge habitats, would expose butterfly populations to additional stresses, such as:

1. increased predation and disease,
2. increased competition for adult and larval resources with edge-loving species,
3. increased insolation (exposure to sun),
4. increased desiccation (wind, lowered humidity, elevated temperatures),
5. air-born pesticides, bio-control agents and other pollutants,
6. inbreeding and resultant genetic drift.

PRESENT OR THREATENED RISKS TO BUTTERFLY AND HABITAT

The continued fragmentation of mature forests, rampant spread of invasive plant species into undisturbed forest remnants, excessive deer browsing and Gypsy moth control efforts all pose imminent threats to the long term survivability of this species. The following discussion outlines the major threats facing this species today, rangewide. Although most of these threats are linked to forest fragmentation, each has its own unique set of circumstances and potential for affecting *Pieris virginiensis*.

Agriculture and Grazing

Agricultural activities affect the West Virginia White in a number of ways. Clearance for row crop production or pasturage removes the habitat entirely, leaving nothing on which the butterfly can survive. Much of this loss occurred in the late 1800's and first half of the 20th century, although localized replacement still goes on. Cattle and swine are (or were) often let loose to forage in forests, feeding on herbaceous vegetation, nuts and fruit. Excessive stocking rates lead to soil compaction and removal of the native forest flora. Despite these negative impacts, Loveland and Hutcheson (1996) state that more than 94 percent of the area designated by Kuchler (1964) as eastern Mixed Mesophytic Forest, has not been converted to agricultural production. However, their analysis stated that logging and other pressure on these habitats still exist.

Insecticides and herbicides used to control pests in agricultural crops can also have negative effects on adjacent West Virginia White populations through direct mortality of both the butterfly (adults and larvae) and the larval foodplants. Several silvicultural pesticides and biocontrol agents are also potentially deleterious to the West Virginia white and/or its foodplants. Additionally, *Dentaria* seeds are dispersed primarily by ants, a phenomenon known as "myrmecochory" (see L'Heureux, 2000). In L'Heureux's Wisconsin study, *Dentaria diphylla* did not occur in secondary forest sites that had re-grown on former agricultural lands. Therefore, the presence of ant populations may be necessary for continued reproductive success in *Dentaria* and establishment on new sites.

Beech Bark Disease

Beech Bark Disease is currently decimating American beech populations throughout the northeast, with mortality as high as 40 percent in some areas (Houston and O'Brien, 1983). The disease occurs when an introduced soft scale insect, the beech bark scale (*Cryptococcus fagisuga* Lind.) causes feeding damage to the bark of larger (>8 inches DBH) beech trees. This allows entry points for either a native fungus (*Nectria galligena*) or an introduced one (*Nectria coccinea* var. *faginata* Lohman, Watson, and Ayers) which then kills the main bole of the tree. Many individuals resprout from the remaining root crown or large lateral roots. However, these are often subject to subsequent attack from elevated scale and fungus populations.

When the primary beech trees die, they leave large gaps in the canopy, allowing increased light to enter the forest floor for a prolonged period of time following spring leaf-out of the remaining trees. While this can potentially enhance the grow of herbaceous species, such as the foodplants of the West Virginia White, these gaps can also provide points of entry for a number of noxious weeds such as poke (*Phytolacca*), Amur honeysuckle (*Lonicera mackii*), buckthorn (*Rhamnus* spp.), autumn olive () and garlic mustard. These highly invasive species compete with both

developing trees and the butterfly's foodplants, further degrading the habitat. If beech comprises a large percentage of the canopy (~>30 percent), increased insolation and wind exposure resulting from their removal may dry out the forest floor or lead to accelerated erosion. This can change the physical and chemical properties of the soil, leading to corresponding changes in the plant species composition of the forest.

Marked declines in beech scale populations occasionally occur over large areas, suggesting that general environmental factors may affect the insect. Air temperatures of -37° C (-15° F) are lethal to scale insects not protected by snow. It is not known whether episodes such as temperature extremes are the only events responsible for population crashes. In addition, from one to five percent of the beech population appears to have bark characteristics making them immune to the effects of the scale insects. Researchers are currently conducting studies to see if the resistant bark characteristics are inheritable.

Natural predators of the scale include a ladybird beetle (*Chilocorus stigma*), which feeds as both larvae and adults on the scale; and the native Carolina weaver cricket (*Campsonotus carolinensis*). The weaver cricket is a large arboreal, aphid and scale eating species known from isolated localities throughout the central and southern hardwood forest regions (Bess, 2004; Blatchley, 1920; Hebard, 1934). LaForest and Lambdin (2000) found that this cricket was the most frequently encountered Orthoptera species in the canopy of mature Tulip Poplars (*Liriodendron tulipifera*) at two sites in a central Tennessee study. This species is likely much more common than records indicate, given its relative restriction to the tree canopy. Another potential biocontrol agent is the fungus, *Nematogonum ferrugineum* (*Gonatorrhodiella highlei*), which parasitizes the nectria fungi (Houston and O'Brien, 1983). The effects of these organisms on the disease agents and on the course of the disease have not been critically evaluated.

Chestnut Blight

Prior to 1900, The American Chestnut (*Castanea dentata*) was the dominant tree species in most dry-mesic, hardwood forest types in eastern North America (see Hough, 1907; The American Chestnut Foundation, 2002). In 1904, an introduced fungus known as the Chinese Chestnut Blight arrived in infected nursery stock. By 1950, this disease had killed over 90 percent of the mature chestnut trees (3.5 billion trees) across nine and a half million acres of forest. This drastically changed canopy composition in our eastern forests, which likely had a variety of effects on the herbaceous layer, including food plants for the West Virginia White where they co-occurred. Positive effects could have been increased insolation and increased plant growth, possibly favoring the butterfly. Negative effects would have included excessive insolation and wind, leading to rapid senescence of the butterfly food plants and death of the developing larvae. Tree seedlings that competed for the spaces formerly held by chestnut would have had varying effects on the future character of the forest, especially with reference to the butterfly. It is likely that effects were mixed and varied according to localized site characteristics such as species composition, slope, aspect and moisture regime.

Climate Change

Weather has profound effects on the productivity of West Virginia White populations. Their host plant tends to be highly ephemeral, so butterflies have a short amount of time in which to complete their life cycle. Long-lasting winter cold of even a few extra days can impact the

likelihood of larvae finding adequate food before the plants senesce (Cappuccino and Kareiva 1985). Similarly, accelerated warming in late spring and early summer can lead to early senescence of the food plants. In Connecticut, late instar (IV and V) caterpillars searching for another food plant during a period of early senescence had only half the density of host plants left in the habitat. Caterpillars had a much greater chance of success in finding a new host plant when the plants were more densely congregated (Cappuccino and Kareiva 1985).

If plants begin to senesce while larvae are still young and relatively sedentary (instars I-III), the larvae become stranded and do not survive. Therefore, human-induced climate change (global warming) should have a combined negative effect on the butterfly by causing increased senescence of the larval food plants, elimination of cold-tolerant species from the forest and the recruitment of plant and tree species that favor warmer, drier conditions. Increased temperatures and reduced moisture levels might also favor certain parasites, predators or disease, further stressing the remaining populations of West Virginia White butterflies.

Competition with Other Species

Pieris virginiensis was (and still is) conspecific with the closely related *P. oleracea* in the northern portions of its range (see Chew, 1980, 1981). However, competition is not considered a factor because of strong habitat segregation: the West Virginia White occurring only in mesic Maple-beech-birch Forests and the Mustard White inhabiting open Canadian Zone Forests and wetlands. In the Midwest, *Pieris oleracea* also inhabits high quality prairie fens south to northern Indiana where it feeds almost exclusively on Watercress (*Nasturtium officinale* L. (Bess, 2004; Nielsen, 1999)). It also appears that *Pieris rapae* does not typically compete with *P. virginiensis* for resources, given the prior's aversion to entering closed-canopy forest (see Cromartie, 1975).

Deer Browsing

Large Predator control efforts in the 19th and 20th Centuries, coupled with poorly managed hunting programs, paid off in an explosion in the size of white-tailed deer (*Odocoileus virginianus*) herds throughout eastern North America. The negative effects of increased (or accelerated) deer browsing on both the herbaceous and shrub flora is being documented in a variety of wooded habitats. This is leading to fundamental changes in both the species and age composition of forest stands and in the composition of the ground flora. Accelerated deer browsing of herbaceous species may be less of a direct threat to the West Virginia white butterfly, because deer tend to avoid *Dentaria* species. In fact, these unpalatable species may respond favorably to deer browsing. However, excessive deer browsing removes adult nectar sources, resting sites and can cause changes to the structure of forests, making them unsuitable for the growth of *Dentaria* or the butterfly.

Disease and Predation

In a Connecticut study, 22% of West Virginia white larvae died from granulosis virus (Cappuccino and Kareiva 1985). Plants that were experimentally covered in soils that were exposed to the virus were associated with greater larval mortality than uncontaminated plants (Cappuccino and Kareiva 1985). This virus builds up in soils and is spread through the host plants. Thus, contamination risk increases over time as plants grow from rhizomes through the same soil each spring. Granulosis epidemics may be responsible for local West Virginia White extinctions that have been otherwise unexplained (Cappuccino and Kareiva 1985). Additional

disease agents will be discussed under a following section (see "**Gypsy Moth Outbreaks and Control Efforts**").

There has also been concern that forest fragmentation may increase access to interior forest by edge-loving species, particularly parasitoids and predators. Many egg and larval parasitoids attack butterflies, particularly the Pieridae. The ubiquitous nature of many of these butterflies has provided a ready supply of hosts for these insects to exploit. Given the fondness of Cabbage Butterflies for a variety of habitats, concern arose that parasitoids specializing on this species could also attack the West Virginia White (see Klots, 1954). While this seems plausible, Benson et al. (2003) found that the Braconid wasp *Cotesia glommerata* L., a parasitoid introduced to control the Cabbage Butterfly, did not appear to attack larvae of *Pieris virginiensis* because the adult females would not forage in closed canopy forest. However, the researchers found that female wasps readily laid eggs on larvae of *P. virginiensis* in laboratory conditions. Fortunately, the Cabbage Butterfly seldom travels into interior forest habitats (see Cromartie, 1975a-b), although it will follow utility rights-of-way and roads into forested areas (Bess, 2004).

Garlic Mustard

Non-native garlic mustard is a severe threat to the long-term survival of the West Virginia White in many areas. This plant is highly adaptable and survives under a broad range of moisture, light and soil conditions (Anderson and Kelley, 1995; Anderson et al., 1996; Brunelle, 1996; Byers and Quinn, 1998; Cruden et al., 1996; Dhillion and Anderson, 1999; Nuzzo, 1993; Roberts and Bodrell, 1983). Garlic mustard overgrows native herbaceous plants, often excluding them from the flora (see Brothers and Springarn, 1992; Luken and Shea, 2000; Luken et al., 1997; McCarthy, 1997; Nuzzo, 1999).

This mustard is commonly oviposited on by female *Pieris virginiensis* and other native whites, although it is toxic to most North American *Pieris* larvae (see Blossey et al., 2001; Bowden, 1971; Chew, 1995; Chew and Renwick, 1995; Courant et al., 1994; Courant and Chew, 1997; Haribal and Renwick, 1998; Huang et al., 19995; Porter, 1994; NatureServe 2004). Larval development on garlic mustard was extremely poor in a population that had exposure to the plant for over 20 years (Courant and Chew 1997). Although it is fond of disturbed situations, garlic mustard can invade relatively pristine plant communities, especially along paths, roadsides and utility rights-of-way (Brothers and Springarn, 1992; Brunell, 1996; Luken et al., 1997; Luken and Shea, 2000; Nuzzo, 1999).

In Monroe Co. Indiana, female *Pieris virginiensis* have been observed ovipositing on garlic mustard in a forested Nature Preserve where *D. laciniata* and *D. heterophylla* are native and patchily distributed (Porter 1994). This phenomenon was also observed on the edges of the Charles Deam Wilderness Area in the Hoosier National Forest, also in Monroe Co. (Bess, 2004). At the latter site, the butterflies were observed along the ecotone between mature maple-beech-birch forest containing scattered *Dentaria* and cultivated fields and fallow land where the garlic mustard dominated.

Gypsy Moth Outbreaks and Control Efforts

Since its introduction into New England in the early 1800's, the Eurasian gypsy moth (*Lymantria dispar*) has posed a direct and indirect threat to native Lepidoptera, including the West Virginia

white butterfly. For many years, the gypsy moth had few predators or parasites here, and its populations soared to outbreak proportions throughout the Northeast (see Schweitzer 2004 for a review). The larvae feed primarily on oaks (*Quercus* spp.) and defoliated countless acres of oak and mixed hardwood forest, including habitat for *Pieris virginiensis*. These defoliation events result in the direct mortality of many other insect species that feed on oak, and change the character of the forest, allowing light to reach the ground flora for a prolonged period of time in early summer. On sites where trees are already stressed by edaphic conditions, repeated defoliation can lead to tree mortality. The leaves that remain or re-sprout have characteristic differing from those on trees that did not experience defoliation (Feeny, 1970; Schultz and Baldwin, 1982; Schweitzer, 1979). The effects of canopy defoliation on the herbaceous flora were documented by Cooper et al. (1993).

Attempts to eradicate the gypsy moth in the mid 20th century involved the use of broad scale organophosphate insecticides such as DDT and Carbaryl. These spraying campaigns covered over 12 million acres in the northern and central Appalachians and affected a wide array of organisms, insects and non-insects alike (Schweitzer, 2004). Chemicals such as DDT also accumulate in successive trophic levels as they pass through an ecosystem. Organisms at the top of food chains (such as insectivores) develop ever-increasing levels of toxins, causing death and/or reduced fecundity. Given the widespread, catastrophic effects of DDT and Carbaryl spraying, these pesticides have been banned in the United States.

In 1976, the growth inhibitor Diflurobenzuron (trade name Dimilin or Vigilante) was registered to control pest insects, while eliminating the indiscriminate poisoning of other organisms (see Schweitzer, 2004). Diflurobenzuron inhibits the formation of chitin, a protein that is the principal component of most arthropod exoskeletons. It only affects young insects, killing them when they go through their next moult ("skin shedding"). Many fungi also contain chitin in their cell walls, and may also be affected (Dubey, 1995). Like the earlier pesticides, Dimilin kills insects (and most other Arthropods) indiscriminately across all orders (see Uniroyal, 1983). The chemical also has a long-lasting residual effect by becoming bound to leaves (particularly conifers) and remaining active even after leaf fall (Martinat et al., 1987; Mutanen et al., 1988; Whimmer et al., 1993). Both aquatic leaf shredders and terrestrial detritivores that feed on these fallen leaves are highly susceptible to this chemical (Bradt and Williams, 1998). Widespread mortality has been documented in the field and laboratory, in both aquatic and terrestrial ecosystems (Bradt and Williams, 1990; Butler et al., 1997; Dubey, 1995; Hansen and Garten, 1982; Lih et al., 1995; Martinat et al., 1987, 1988a-b; 1993; McCasland et al., 1998; Mutanen, et al., 1988; Reardon, 1995; Swift et al., 1988).

Bacillus thuringiensis (*Btk*) is a relatively new threat to the butterfly, introduced in the fight to control Gypsy moth outbreaks in the early 1970's. *Btk* is a naturally occurring soil pathogen that is stated to affect only Lepidoptera larvae, causing high rates of mortality in exposed individuals across many families (Peacock et al., 1998). The bacterium attacks the lining of the gut wall, interrupting the uptake of nutrients by the affected caterpillar, causing starvation and death. *Btk* spraying for both gypsy moth and spruce budworm control is known to have long-lasting, deleterious effects on resident populations of non-target Lepidoptera (Boettner et al., 2000; Butler et al., 1995, 1997; Cooper et al., 1990; Hall et al., 1990; Herms et al., 1997; Johnson, et

al., 1995; Krieg and Langenbruch, 1981; Miller, 1990; Morris, 1969; Schweitzer, 2000, 2004a-b; Severns, 2002; Wagner, 1995; Wagner et al., 1996; Whaley, 1998).

Although gypsy moth outbreaks tend to occur in oak-dominated forests, many beech maple forests contain large amounts of oak (esp. *Quercus rubra*). The larvae of this moth also feed readily on beech, basswood, maples and a number of other species occurring in Maple-Beech-Birch forests. Given the coincidental occurrence of gypsy moth and West Virginia white larvae in late May and June, large scale spraying efforts within the range of the butterfly have likely played a role in reducing its overall population size and distribution, especially in the 1950's and 1960's. Btk is currently the preferred control agent for outbreaks of the gypsy moth and in Wisconsin alone, more than 250,000 acres will be sprayed in 2004 (see USDA, 2004a).

These control efforts not only indiscriminately kill countless insects, but have long-lasting effects on habitats that are sprayed. The loss of caterpillars to feed their young has been shown to negatively affect fecundity and body weight in nesting birds, bats and small mammals (Bellocq et al., 1992; Cooper et al., 1990; Holmes, 1998; Sample, 1991; Sample et al., 1993a-b, 1996; Seidel and Whitmore, 1995; Whitmore et al., 1993a-b; Williams, 2000). This effect is typically carried over through at least a second year, mimicking the reduction in observed Lepidoptera larvae during the season of application. Given that gypsy moth larvae develop at the same time of year as the West Virginia White, spraying of *Btk* or other pesticides in occupied habitat could certainly have a negative effect on the resident butterfly population.

Currently, a fungus (*Entomophaga maimaiga*) has been introduced in the war on gypsy moths (see Hajek, 1998; McManus et al., 1989; Reardon and Hajek, 1998). The fungus appears to be specific to butterfly and moth larvae, particularly the family Lymantriidae, which contains the gypsy moth (see Wallner, 1989). However, in laboratory bioassays of non-target insects, other larvae were found to be susceptible (Hajek et al., 1995, 1996, 2000). This is particularly true for those with a granular skin surface or coating of short, dense hairs, e.g. all Lymantriidae; the Noctuidae genus *Catocala*. The larvae of the West Virginia white also fit this description and, although not tested for susceptibility, should be considered potentially sensitive to infections by the fungus. Another fairly specific control agent is the gypsy moth nuclear polyhedrosis virus (trade name Gypchek). This virus is also supposedly specific to Lymantriidae and particularly the gypsy moth (Reardon et al., 1995). A recent, non-lethal, control method is the use of pheromones (trade name Disparlure) to disrupt mating in the gypsy moth. This chemical is specific to the Lymantriidae and is not known to affect other Lepidoptera.

Over Utilization

Direct over utilization of the West Virginia White Butterfly would come primarily in the form of over collecting for specimens by Lepidopterists. While this could pose a significant problem for small, isolated colonies; there are several large, well-known "metapopulations" on public lands spread throughout the range of this species (see following Sections). Currently the species is not heavily sought after by collectors of the rare and unusual. Therefore, over collecting is not currently thought to pose a threat to the long-term survival of this species, although it could if populations continue to decline and habitat continues to be lost to human development, invasive species and disease.

Forest clearing and fragmentation appear to be the greatest threats facing this species. Prior to and during the early European settlement of our nation, mature maple-beech-birch forests were utilized for a variety of resources; timber, home sites, game, maple syrup, nuts, fruit and a variety of native plants used as herbal medicines (Erichsen-Brown, 1979; Facciola, 1998; Mooreman, 1998; Thomas and Schumann, 1993). As the colonial populations grew, large tracts of forest were cleared for timber and growing agricultural crops. This practice was heavily accelerated in the mid-1800's (Foster and O'Keefe, 2000; Leverett, 2001; Ritters et al., 2002). By 1950, much of the once vast hardwood forest that blanketed the eastern half of the United States was gone (Eyre, 1980; Hutchinson, 1996; Kuchler, 1964; Leverett, 2001; Ritters et al., 2002).

From the early 1900's until present time, efforts have been undertaken on both the state and national level to begin re-forestation of much of this cleared land. In Ohio for example, many of the current state forests were begun as re-forestation projects on vast acres of prior agricultural land. Overall acreage of many hardwood forest types has increased over the past 100 years through a reduction in logging, suppression of wildfires and a general shift towards the use of pine in construction. However, many early re-forestation projects involved replanting former hardwood areas with pines, a more commercially valuable timber at the time. This further reduced the remaining acreage of maple-beech-birch forest and hampered future restoration efforts.

Many re-planted or successional tracts are also young (<50 years old) and have species compositions that may or may not resemble the original forest. Often, the native herbaceous flora has been severely altered or removed through excessive grazing by livestock, especially hogs. Overgrazing and repeated logging also causes soil compaction, altering its water-retention qualities and increasing runoff of surface water. Cover by Eurasian grasses planted as pasture forage may also play a factor in recruit establishment and ultimate forest characteristic.

Residential Development

Residential Development affects West Virginia White in a variety of ways. The clearing of sites for houses and associated roadways eliminates habitat and divides what remains into highly isolated islands, separated by paved streets, parking lots, lawns and other habitats inhospitable to the butterfly. Lawn development and maintenance eliminates the native flora, and drift of herbicides and insecticides has a cumulative effect in deteriorating what remains in adjacent natural areas. Fertilizer and pesticide runoff can also contaminate adjacent natural areas, enter streams and rivers and degrade local and regional water quality. In the Northeast and Upper Midwest, high-end and exclusive residential developments are often located in remnants of mature maple-beech-birch forests.

Roadway and Utility Right-of-Way Development and Management

Roadways and utility rights-of-way can act as obstacles to the dispersal of West Virginia White butterflies between patches of suitable habitat (Cappuccino and Kareiva, 1985). The butterfly does not typically venture into treeless environments such as fields or wide, mowed roadways or utility corridors. They will, however, venture down small dirt roads, intermittently maintained trails, utility corridors and pathways, when tree cover is partial and either larval food plants or adult nectar sources are present. The most common activities associated with these linear human

structures have the greatest potential to harm the West Virginia White; maintenance. Mowing and herbicide spraying (common grounds maintenance activities) can have a deleterious effect on both habitat and the foodplants of the butterfly, when conducted haphazardly.

Silvicultural activities

A number of silvicultural activities can have negative effects on the West Virginia White, including:

1. clear cutting of hardwood stands,
2. replanting of former hardwood stands to conifers,
3. use of biocontrol agents such as *Btk* and *Maimaiga* to control forest pest insects, and
4. development of roads, parks and other intense human-use areas in mature maple-beech-birch forest remnants.

In the past, small (~20-40 acre) clear cuts were probably not a severe threat to this species and may have even provided additional, temporary foraging habitat for adults along the edges. However, the current landscape of scattered islands of forest in a sea of intensely altered, treeless habitats, is an impediment to the dispersal of West Virginia White butterflies between areas of suitable habitat. Continued clear cutting of mature hardwood forests will further reduce the size, distribution and connectivity of West Virginia White populations. The increased proportion of edge habitat in fragmented forests also provides additional access points for edge-loving predators, parasites and invasive species. Finally, conifer plantations in former hardwood areas, while a necessity for numerous industries, also have a negative effect in reducing the amount and quality of potential habitat for this butterfly. The effects of conifer plantations on the butterfly's dispersal are undocumented.

INADEQUACY OF EXISTING REGULATORY MECHANISMS

The current, species-based approach to federal laws regarding the protection of imperiled organisms does not currently afford legal protection to the West Virginia White butterfly. An ecosystem or plant community based approach would be more adequate for the protection of organisms whose habitats are becoming increasingly fragmented and degraded by human activity. This is especially true for species requiring mature forests, such as the West Virginia white.

SUMMARY OF LAND OWNERSHIP & EXISTING HABITAT PROTECTION

CURRENT LAND OWNERSHIP OF *PIERIS VIRGINIENSIS* HABITAT

Figure 3 clearly shows that the vast majority of the remaining tracts of maple-beech-birch forest types occur on non-federal lands. However, throughout the current range of this species, numerous Federal and State Forests contain large amounts of mature maple-beech-birch forest (see "**STATE AND NATIONAL FOREST DISTRIBUTION**"). In many instances (and particularly in the southern Appalachians), the bulk of known butterfly populations are also recorded from public lands. Public and private universities, Conservation Organizations and Land Trusts also hold tracts of old-growth forest, some of substantial size. Of the remaining old

growth forest in the eastern United States, more than 50 percent is in private hands (Eastern Old Growth Clearinghouse, 2004).

CURRENT LEVEL OF HABITAT PROTECTION

Nearly all of the West Virginia White populations in the southern Appalachians occur on National Forest and National Park Service lands (see Figure 4). A majority of the populations in Michigan and Wisconsin also occur on National Forest lands. See "**STATE AND NATIONAL FOREST DISTRIBUTION**" for a listing of potential and known public lands containing populations of this species. The Forest Service designation of "Regional Forester Sensitive Species" provide for protection for this (and other) species on Forest Service lands by involving them in the planning phase of various forest activities that may impact their habitat. There has also been a growing movement within the Service to protect and manage for old growth forest, further providing protection for habitat of this species. On-going efforts to designate Roadless Areas, Special Areas and Research Natural Areas also provides habitat protection for the butterfly. In particular, the Forest Service Roadless Area policy has protected thousands of acres of forest from wheeled vehicles, limiting greatly the ability of invasive species to penetrate interior forests along these lines of disturbance. As outlined in previous sections, numerous State Forests and State Parks contain either suitable habitat or known populations of the butterfly throughout its range.

SUMMARY OF EXISTING MANAGEMENT ACTIVITIES

Current management activities aimed directly at the protection of West Virginia White butterflies are few. The species usually benefits from the designation of Special Areas or Roadless Areas aimed at protecting old growth hardwoods. The recent invasion of the Nation's hardwood forests by garlic mustard has prompted a fairly intensive effort to begin controlling and hopefully eliminating this species from high quality forest tracts (see Luken and Shea, 2000; Luken et al., 1997; McCarthy, 1997; Nuzzo, 1999; Porter, 1994; USDA, 1997). Given the multiple negative effects this plant has on the West Virginia White butterfly and its habitat, it can only stand to benefit from garlic mustard eradication efforts.

The introduced invasive shrubs, Amur honeysuckle (*Lonicera mackii*) and glossy buckthorn (*Rhamnus cathartica*), have also blanketed and degraded thousands of acres of potential habitat for this species across much of eastern and central North America (McKnight, 1993; . Numerous land managers continue to eradicate these shrubs from mature forest remnants, enhancing potential habitat for the butterfly and other species (see . Fire, although a very sporadic disturbance (probably 50-300yr intervals) may have also played a limited role in the maintenance of habitat for *Pieris virginiensis*. The clonal nature of the larval foodplant, its early senescence and subterranean rootstocks would tend to make it a fire neutral or fire positive species. However, overwintering pupae of the butterfly would be very sensitive to mortality through immolation. Research on fire effects in maple-beech-birch forest is limited, especially with respect to the effects on *Dentaria* and *Pieris virginiensis* (see Luken and Shea, 2000; Gorman, 2004; Schwartz and Heim, 1996).

PAST AND CURRENT CONSERVATION ACTIVITIES

CONSERVATION OF HABITAT

Across its range, many of the known West Virginia White populations occur in remnants of mature hardwood forest on state owned and managed lands. Roadless Area and Special Area designations within these holdings have also protected habitat for this species.

For the bulk of mature, Maple-beech-birch-Birch forest that remains on private lands, many states within the range of the butterfly have begun forest registry and stewardship programs to assist landowners. These programs facilitate the protection and sensible management of privately owned forest tracts, often specifically targeting old-growth hardwood forest types. The National Forest Stewardship Program, passed by Congress in 1990, is an example. This program was adopted from the Alabama TREASURE Forest Program, begun in 1974, which "seeks to promote sound and sustainable, multiple-use forest management. This type of management encourages landowners to use their forests wisely to meet their own needs while at the same time protecting and enhancing the environment".

CONSERVATION OF *PIERIS VIRGINIENSIS*

The West Virginia White is increasingly a species of concern for conservation because of continued habitat loss and the negative effects of invasive plant, insect and fungal species. This increasing rarity, and its association with an imperiled and visually appealing habitat, has resulted in public campaigns to aid its protection. Several State Nature Preserves have been developed or expanded specifically to include habitat for this species. The Nature Conservancy currently assigns *Pieris virginiensis* a Global Rank of G3, a recent upgrade from G4, meaning it is considered imperiled throughout much of its former range. Currently, this butterfly is listed as a species of conservation concern in the following States and Provinces (as):

Canada

Ontario (Endangered)

United States

Indiana (State Rare)

Wisconsin (Special Concern)

SURVEYS AND MONITORING

RECENT STATUS SURVEYS

Recent state-level surveys to assess the status of *Pieris virginiensis* have been undertaken in Indiana (Bess, 2004), New York (Stanton, 2001) and Wisconsin (see Cheq-Nic 2004). Only Connecticut and Kentucky currently consider this species to be secure from extinction within their boundaries. The West Virginia white is extirpated in NJ and imperiled in Pennsylvania (NatureServe 2004). It is listed as vulnerable in IN, MA, MD, NC, ON (Canada), OH, TN, VA and WV. Other states within the range of this species are in the process of evaluating its status and include MI, AL, GA, SC, NY, VT and QC (Canada). Given its limited geographic range within each state, *Pieris virginiensis* should receive a ranking of S1 or S2 for AL, GA and SC.

SURVEY PROTOCOL

Surveys should be conducted during the adult brood, the timing of which will vary based on latitude and altitude. The adults are relatively easy to identify, although a voucher specimen should be collected at all new locations for this species. The adults can be confused on the wing with other white butterflies such as *Pieris rapae* and *P. oleracea*. However, *P. rapae* almost always has dark spots on the dorsal forewings and the underside is flush with lemon yellow, as in *P. oleracea*. *P. oleracea* can be distinguished from *P. virginiensis* by the characters given previously in this report (see Figures 1 and 2). Surveyors should carry a net while walking through areas of potential habitat. Choose warm (>60F), sunny days with a minimum of wind (<15 mph) and cloud cover (<50 percent). Concentrate surveys around known populations of *Dentaria* and adult nectar sources (see Yahner, 1998). Any observed adults should be netted to verify identification and to collect a small (<4), initial voucher series.

IDENTIFICATION OF ADDITIONAL POPULATIONS

Currently, large tracts of unsurveyed, mature maple-beech-birch forest remain on steep hillsides, in ravines and along riverbottoms throughout Indiana, Kentucky, Tennessee and Michigan. No confirmed records for the West Virginia white are known from Illinois, Maine, Minnesota, New Hampshire or the Ozarks of Arkansas and Missouri, although suitable habitat exists in all. Coincidentally, *Dentaria diphylla* is native to New Hampshire and Maine, while *D. heterophylla* has a disjunct series of populations in the mountains of west-central Arkansas. These areas would be prime targets to survey for additional West Virginia White populations. However, neither *Dentaria diphylla* nor *D. heterophylla* are known from Illinois and no *Dentaria* species are on the most recent Minnesota plant list (MNDNR, 2002).

Surveys should be undertaken during the known flight season of adults, based on the nearest populations. Surveys can be conducted on warm (>60F) days with a minimum of wind (<15 mph) and cloud cover (<50 percent). Concentrate surveys around known locations of the primary foodplants, *Dentaria diphylla* and *D. heterophylla*. At sites where these plants do not occur, but the butterfly is known nearby, Search near populations of *Dentaria laciniata* and/or *Arabis laevigata*. At each new location for the species, from one to four adult voucher specimens should be collected, labeled with appropriate collecting data (at a minimum, date, specific location, collector) and deposited in a state or nationally housed insect collection. Identification of all specimens should be verified by an expert (see Contacts at the end of this Document).

LONG-TERM POPULATION MONITORING

To track the dynamics of known West Virginia White populations over time, a long-term monitoring program will need to be developed (see Pollard, 1977). Monitoring programs will naturally vary from site to site and depend greatly on the amount of resources available to conduct such programs. At a minimum, a long-term monitoring program for *Pieris virginiensis* should involve the designation of at least one permanent, butterfly monitoring transect. Monitoring transects should pass through all representative habitats at a site, with emphasis placed on closed canopy hardwood forest.

MONITORING PROTOCOL

The monitoring transect should be of a length that can be covered by one or two observers in one to two hours, while walking at a moderate pace. All *Pieris virginiensis* observed within 30 feet of the transect line should be counted and their sex and flight condition (freshly emerged, slightly worn, badly worn) noted. Information on behavior should also be noted, such as nectaring, ovipositing, mating, resting, etc. Standardized survey forms can easily be developed and a sample is attached as Figure 5. At a minimum; transect name, location, date, time, temperature and cloud cover should be noted on each survey form. Information on plant phenology, species blooming, canopy cover, invasive species, predation, etc. is also useful. Surveys should be conducted every day with suitable weather conditions for the duration of the flight period. These surveys provide a wealth of data for use in tracking long-term population shifts in size, phenology, distribution and resource utilization.

LONG-TERM RESEARCH PRIORITIES

The following are some broad categories of necessary, critical long-term study regarding the West Virginia white butterfly;

1. Minimum forest size requirements for sustainable populations of both butterfly and foodplants;
2. Effects of canopy disturbance (e.g. logging, gypsy moth defoliation, beech bark disease) on populations of butterfly and foodplants.
3. Effects of *Btk*, *Maimaiga* and other gypsy moth bioagents;
4. Effects of garlic mustard invasion and subsequent control efforts on both butterfly and foodplant populations; and
5. Effects of global warming on habitat, butterfly and foodplants.

INSECT SPECIES OF CONCERN ASSOCIATED WITH *PIERIS VIRGINIENSIS*

Federally Protected Species and Federal Species of Concern

A number of notable insect species are associated with Maple-beech-birch forests and *Pieris virginiensis*. These include the Six-Banded Longhorn Beetle (*Dryobius sexnotatus*), a Federal Species of Concern (FSC), and the Federally Endangered American Burying Beetle (*Nicrophorus americanus*). The Six-Banded Longhorn feeds as a larva on newly dead or dying maples, boring into the wood. Adults can sometimes be found under bark on dead logs and do come to light. This beetle was known historically from many eastern states but appears to have undergone a rangewide population crash in the 1960's. Few modern records exist and most come from central Indiana (J. Zablotny, 1996 pers. comm.). It is associated with large tracts of old-growth maple-beech-birch forests with many over-aged and wind thrown trees. Forest

fragmentation and widespread spraying of DDT and Carbaryl in the 1950's are suspected as leading causes in the decline of this species.

The American Burying Beetle was also historically common across eastern North America, but practically disappeared by the late 1960's. It was thought extinct until recently, when isolated populations were discovered in the Ozarks of Arkansas and Oklahoma, and on Block Island off the coast of Rhode Island. The decline of this species is thought by some to be tied to the extirpation of the Passenger Pigeon, although there is a ~30 year gap between the crash of the Passenger Pigeon and that of the beetle. Direct mortality from widespread DDT and Carbaryl spraying in the 1950's, coupled with the decimation of other native bird populations by DDT poisoning in the 1950's-70's, are more likely reasons for the beetle's decline. Both of these insects are quite large and were readily collected in the past by amateurs and professionals alike. Their abrupt disappearance from the landscape suggests a major shift in the regional environment during the middle of the 20th century. This corresponds with the widespread use of organophosphate insecticides, particularly for the control of mosquitoes and the gypsy moth.

The Diana Fritillary Butterfly (*Speyeria diana* (G3: FSC)) is another Federal Species of Concern that experienced a widespread population decline in the 1960's and 1970's. This once widespread butterfly disappeared from southern Illinois, Indiana and western Kentucky. Many long-known populations in the central Appalachians also disappeared or declined dramatically. Widespread deforestation had slowed, given the relative inaccessibility of the remaining forest tracts, and the Diana Fritillary was still considered locally common throughout the central and southern states. Therefore, it is quite likely that insecticide spraying for the control of forest pests, particularly the gypsy moth, led to the elimination of this butterfly from many sites. Currently, the use of Btk for gypsy moth control also endangers the Diana Fritillary, as the larvae are feeding at the time of gypsy moth spraying and are highly susceptible to infection by this bacterium, with high rates of mortality.

Other Butterfly and Moth Species of Concern

A variety of globally imperiled butterfly species co-occur with the West Virginia White butterfly. These include; the Golden Banded Skipper *Autochton cellus* (G4), Appalachian Azure *Celastrina neglectamajor* (G3G4), The Smokey Azure *Celastrina nigra* (G3G4), Harris's Checkerspot *Chlosyne harrisii* (G4), Early Hairstreak *Erora laeta* (G3G4), Western Pine Elfin *Incisalia eryphon* (G5), Bate's Crescent *Phyciodes batesi* (G3) and the Appalachian Green Anglewing *Polygonia faunus smythi* (G5:T3T4). Globally imperiled moths associating with the butterfly include; Hebard's Stoneroot Flower Moth *Erythroecia hebardii* (G1G3), Astute Stoneroot Borer Moth *Papaipema astuta* (G3G4), Golden Borer Moth *P. cerina* (G4), Duplicate Stoneroot Borer Moth *P. duplicata* (G2G4), Cup Plant Borer Moth *P. polymniae* (G3G4), Arrowwood Prominent Moth *Schizura badia* (G4) and the Red Legged Tiger Moth *Spilosoma latipennis* (G3).

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APPENDIX

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FIGURES

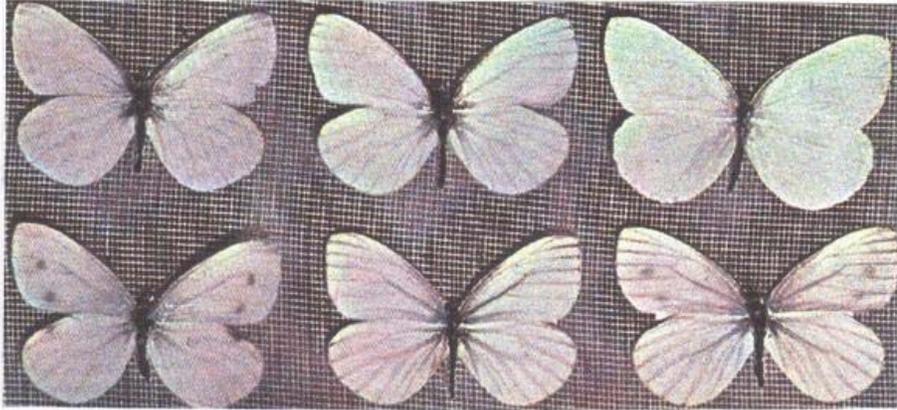


Figure 1. *Pieris virginiensis* (left) and *Pieris oleracea* (center and right). Dorsal surface.
(adapted from Hovanitz, 1963)



Figure 2. *Pieris virginiensis* (left) and *Pieris oleracea* (center and right). Ventral Surface.
(adapted from Hovanitz, 1963)

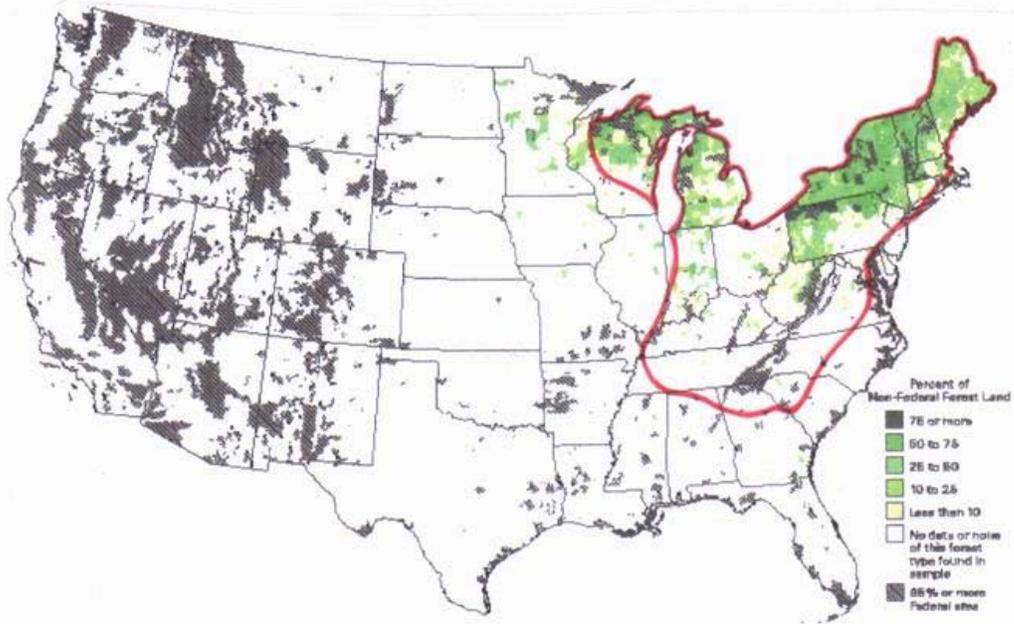


Figure 3. Hypothetical historic (ca. 1800) distribution of *Pieris virginiensis* and current distribution of Maple-Beech-Birch Forests. (base map adapted from NRCS, 1996).

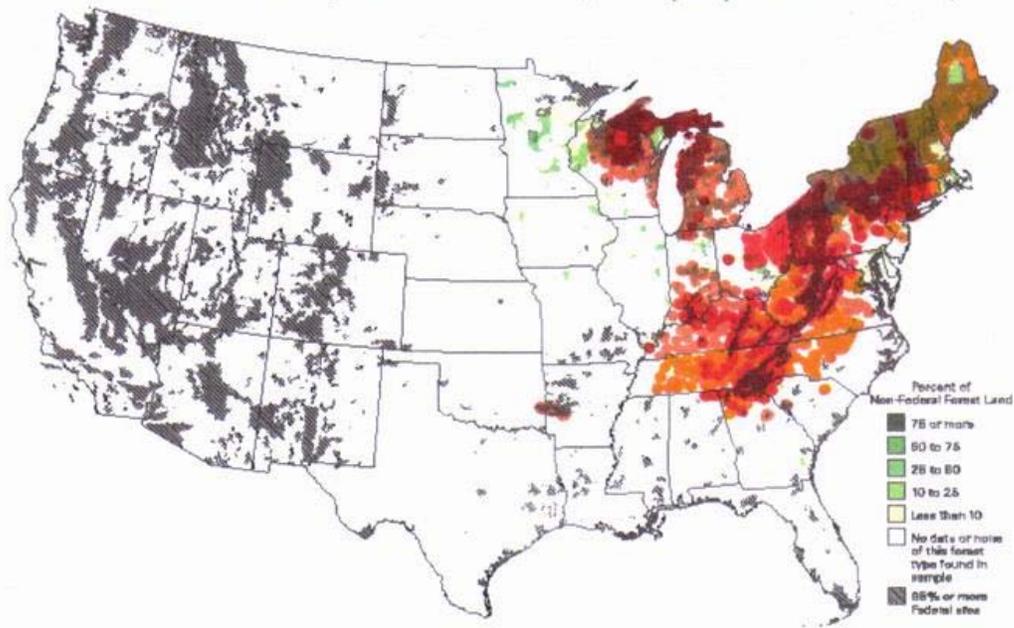


Figure 4. Current distribution of *Pieris virginiensis* (●) and its two major foodplants (●), *Dentaria diphylla* and *D. heterophylla*.

