Conservation of butterflies in an era of global climate change



Karner Blue butterfly, female (left), male (right). Wilton Wildlife Preserve and Park, New York. Photos by Aleta S. Wiley

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1. Abstract

In the last few years, climate change has pushed to the forefront of threats to the natural environment. Global temperatures are predicted to increase by 1.4°C to 5.8°C in the next century. Scientists and environmentalists are racing to determine how these changes will affect wildlife, habitat, and our natural resources. Butterflies are an exemplary species for studying how climate change will affect populations, and numerous studies already have been conducted to record observed changes in certain species and to forecast future changes through bioclimatic modeling. The first part of this paper provides an overview of the status of butterfly populations worldwide and summarizes current strategies for conserving threatened species. A literature review follows of recent research that has improved our knowledge about how changes to the climate will affect butterflies. This paper concludes with two case studies and recommendations for future conservation.

2. Introduction

Over the past century, the challenges faced by conservationists in striving to preserve habitat, biodiversity, and natural resources have changed as new threats emerged. Each time a new threat to the environment is identified, communities struggle to determine how best to avoid environmental disaster, and while one challenge might be overcome in one area, it might still pose a threat somewhere else. In some examples, pollutants and chemicals have been the major threat to wildlife and clean resources, like air and water. Other times, habitat fragmentation and urban sprawl were the focus of discussion. Hunting, over-consumption, and illegal trade in wildlife have all been major obstacles that conservationists have attempted to overcome. All of

these threats continue to require close attention and consistent adaptive management by all individuals working to protect the environment.

In recent years, the threats of global climate change have necessitated the development of new, creative solutions to protect our valuable resources. Climate change is occurring as the amount of carbon dioxide (CO_2) in the atmosphere increases, which leads to global warming by trapping additional solar energy near the Earth's surface (Root and Schneider, 2002). These increased temperatures are causing a variety of changes around the globe, including melting sea ice and more extremes in weather, such as significant draughts (Root and Schneider, 2002). These detrimental effects of climate change are occurring globally and completely independent of where increased CO_2 emissions are being released. It is vital that this new challenge faced in the 21st century be addressed globally. Nations must work together to complete comprehensive research and to help initiate comprehensive management plans on the ground to preserve biodiversity from impending threats of global climate change.

According to the Intergovernmental Panel on Climate Change (IPCC) (2001), average global temperatures are expected to rise $1.4^{\circ}C - 5.8^{\circ}C$ in the 21^{st} century. However, this rise will not occur at a constant rate across space or time (Root and Schneider, 2002). Any rise more than $2^{\circ}C - 3^{\circ}C$ is predicted to cause serious changes to the environment (Root and Schneider, 2002). In some areas, minimum, winter temperatures are rising twice as fast as maximum, summer temperatures (Crozier, 2003). In Germany and the United Kingdom, temperatures are more variable in the first half of the year compared to late summer and fall temperatures (Menzel and Sparks, 2006). These temperature changes will cause a host of problems, including melting glaciers that will reduce freshwater in watersheds, rising sea levels, increased drought, and coral bleaching. Also, even as the general climate faces temperature increases, some microclimates are

going to face temperature decreases. As plants start growing earlier in the spring, they will create more shaded habitat earlier in season, leading to microclimatic cooling (Wallisdevries and Van Swaay, 2006).

Effects of these climate changes on organisms already have been documented. In a largescale, meta-study that included research on 143 different species of diverse taxa, more than 80% had demonstrated range shifts in the direction expected due to climate change (Root, 2003). Even if temperatures increase at a constant rate, the risk of extinctions increases exponentially (Hoyle and James, 2005). One problem with trying to predict the effects of climate change on wildlife is that these effects will depend on how quickly certain species can evolve or adapt by phenotypic plasticity in response to these changes to their environment (McCarty, 2001).

Butterflies provide an excellent example for examining the kinds of effects that climate change will have on biodiversity. They are relatively well studied in some areas of the world; they have been the focal species observational studies, experimental, controlled experiments in greenhouses, and predictive modeling projects. In fact, in 1993, a comprehensive book on butterflies and climate change included topics such as atmospheric systems, life history traits, adaptations to climate changes, and evolutionary history (Dennis, 1993).

The goal of this paper is to use research published since the publication of this book to provide a comprehensive overview of the varying effects of climate change on butterflies around the world. However, first, a review of the status of butterfly populations and of the reasons why conserving these taxa is so important is included. Then, after a general discussion of the major changes expected for butterfly populations, two case studies are provided to illustrate these effects. Finally, I provide some recommendations for incorporating the threats of climate change into conservation plans aimed at preserving butterfly diversity.

3. Butterflies

3.1. ECOLOGY

Taxonomically, butterflies are insects from two super-families, Papilionoidea and Hesperioidea, within the order Lepidoptera, which also includes moths. Papilionoidea are the "true" butterflies while Hesperioidea are skippers. There are several families of butterflies; however, more than 80% of all species are in one of three major families: Hesperiidae (skippers), Nymphalidae (morphos, milkweeds, fritillaries), and Lycaenidae (blues, hairstreaks, and coppers) (New, 1997).

All butterflies go through four stages of metamorphosis: first, an egg is laid, which can hatch either before or after winter, depending on the species. Then, the larva feeds on plants until it forms a chrysalis, the pupal stage. Finally, the pupa will emerge as an adult butterfly. Different species have different generation times, and different numbers of broods per year. Species tend to have more broods per year in warmer areas (Pyle, 1981). Some species overwinter as an egg, while others survive the winter as larvae or pupae. Adult butterflies can spend up to 20% of their time foraging for nectar (Wiklund and Ahrberg, 1978). Other time is spent searching for mates and remaining sheltered during rainy or windy weather.

Worldwide, there are an estimated 10,000-20,000 species of butterflies that occupy habitats from rainforests to grasslands to wetlands (Pyle, 1981). All these species have adapted various traits to protect them from predators, such as birds and lizards (Pyle, 1981). Butterflies are known for their elaborate coloration, which can serve to camouflage them in their surroundings, to warn predators that they are toxic, or to communicate with conspecifics. Many examples also occur of non-toxic species mimicking the coloration of toxic species, such as the

Viceroy copying the Monarch or the Red-spotted Purple mimicking the Pipevine Swallowtail (Pyle, 1981).

Butterflies are often categorized as either mobile or sedentary, depending on how well they disperse over large areas of habitat. They are also either generalists or specialists, which depends on whether the larvae feed on multiple species of plants or if they specialize on one species for a host plant. These traits are highly correlated; for example, in Britain, all generalists are also mobile (hence the common phrase, "mobile-generalist"), and 26 out of 28 species that specialize on one host plant are sedentary (Warren, 2001).

Scientists have focused on butterflies to study ecological questions, including mimicry, sexual selection, and insect-plant interactions. The metapopulation concept in particular has been applied to populations of butterflies. The theory of metapopulation dynamics describes how populations of populations can survive even if local populations are extirpated (Levins, 1970; Gilpin, 1991). Independent patches of habitat support different numbers of individuals at any given time. As a result of local extirpations, some patches may not support populations for some time. However, as long as other populations survive elsewhere, there is the possibility for a vacant patch to be re-colonized.

Additional research on the ecology and behavior of butterflies has included experiments on edge effects and of the use of habitat corridors. Corridors might help to preserve natural habitat by connecting patches so that individuals can disperse over larger areas. Ries and Debinski (2001) studied the responses of two species of butterflies, a habitat specialist, the Regal Fritillary, and a habitat generalist, the Monarch. While the habitat specialist tended to respond strongly by turning around when it approached all types of edges, such as fields and roads, the habitat generalist only responded strongly when it encountered a tree line. Haddad (1999)

hypothesized that a butterfly's behavior at a habitat edge could indicate how much it would use a corridor. If the butterfly did not cross edges, corridor use would be higher since it would search its landscape only for the habitat for which the butterfly is adapted. He expected specialists to use corridors more often than generalists. In fact, his results showed that specialists were 3-4 more times likely to turn back into a patch when they approached habitat edges, and they were more likely to leave a patch only through a corridor.

3.2. CURRENT STATUS

Searches of the primary literature on butterflies reveal the dominance of research performed in the United Kingdom and the United States, compared with other areas of the world. Even though 10,000-20,000 species of butterflies are estimated to occur in the world, only 700 of these are in the United States and only 56 native species occur in the United Kingdom (Fox et al. 2007). Larsen (1995) compiled species counts by biogeographical region and found, out of a total of 18,000 species worldwide, 8,000 were Neotropical, 3,600 were Afrotropical, and only 700 were from the Nearctic. When considering papers published specifically on the conservation of butterflies, few concern species from outside these two countries, with Canada, Australia, and the Netherlands providing most of the exceptions. No published articles were found that dealt specifically with the effects of climate change on butterfly populations outside of the United States or United Kingdom. Despite this lack of research, concern for the effects of climate change should be greater for these populations since species' ranges tend to be smaller in the tropics than in more temperate environments (Pimm, 2001).

In 1973, the United States passed the Endangered Species Act (ESA), which has been one of the most important pieces of legislation to help protect habitat and to prevent other anthropogenic causes of population decline in numerous species of wildlife and plants. As of

2007, the United States Fish & Wildlife Service (US FWS) had listed 19 species or subspecies of butterflies under the ESA. Eleven of these species occur only in California, six of which were listed together in 1976 (see Table 1).

California is ecologically isolated by desert, mountains, and ocean and, therefore, has a high proportion of endemic species (Arnold, 1983). The six species listed in 1976 are all in the Lycaenid family and occur in coastal habitats. Five of the six species were restricted to only a few isolated patches at the time they were listed (Arnold, 1983). Mark-recapture studies revealed that there was infrequent movement between patches for these species, further causing alarm that the five species might be extirpated in the near future (Arnold, 1983).

Table 1: US FWS Threatened and Endangered Species (Butterflies)				
COMMON NAME	SCIENTIFIC NAME	LOCATION	YEAR LISTED	
El Segundo Blue	Euphilotes battoides allyni	CA	1976	
Lange's Metalmark	Apodemia mormo langei	CA	1976	
Lotis Blue	Lycaeides argyrognomon lotis	CA	1976	
Mission Blue	Icaricia icarioides missionensis	CA	1976	
San Bruno Elfin	Callophys mossii bayensis	CA	1976	
Smith's Blue	Euphilotes enoptes smithi	CA	1976	
Schaus wallowtail	Heraclides aristodemus ponceanus	FL	1976	
Palos Verdes Blue	Glaucopsyche lygdamus palosverdesensis	CA	1980	
Oregon Silverspot	Speyeria zerene hippolyta	CA, OR, WA	1980	
Bay Checkerspot	Euphydryas editha bayensis	CA	1987	
Mitchell's Satyr	Neonympha mitchellii mitchellii	IN, MI, OH	1991	
Umcompahgre Fritillary	Boloria acrocnema	СО	1991	
Myrtle's Silverspot	Speyeria zerene myrtleae	CA	1992	
Karner Blue	Lycaeide melissa samuelis	8 Great Lake states	1992	
Saint Francis' Satyr	Neonympha mitchellii francisci	NC	1994	
Behren's Silverspot	Speyeria zerene behrensii	CA	1997	
Quino Checkerspot	Euphydryas editha quino	CA, Mexico	1997	
Callippe Silverspot	Speyeria callippe callippe	CA	1997	
Fender's Blue	Icaricia icarioides fenderi	OR	2000	
US FWS Threatened and Endangered Species System (TESS), 6/1/2007				

The United Kingdom has monitored its 56 species of butterflies closely, and no species was endemic to the area as of 1993 (Pollard and Yates, 1993). Since 1976, the UK Butterfly Monitoring Scheme has coordinated these efforts. Currently, conservation efforts for 11 of these "Priority species" are guided by Biodiversity Action Plans (see Table 2). According to Butterfly

Conservation, one of the primary organizations devoted to preserving butterflies and moths in the United Kingdom, three of the protected species should be demoted to "Species of Conservation Concern". The Silver-spotted Skipper and the Adonis Blue have had an increase in abundance, and the Large Copper has been extirpated in the United Kingdom (Fox et al., 2007). The report also proposed that an additional sixteen species be added as Priority species under the Biodiversity Action Plans. According to the report, among the 24 species identified for conservation priority, three are threatened specifically by climate change: the Northern Brown Argus, the Glanville Fritillary, and the Mountain Ringlet (Fox et al., 2007).

Table 2: United Kingdom Biodiversity Action Plans (Butterflies)				
COMMON NAME	SCIENTIFIC NAME	NOTES		
High Brown Fritillary	Argynnis adippe			
Northern Brown Argus	Aricia artaxerxes	Direct threat from climate change		
Peal-bordered Fritillary	Boloria euphrosyne			
Chequered Skipper	Carterocephalus palaemon			
Marsh Fritillary	Eurodryas aurinia			
Silver-Spotted Skipper	Hesperia comma	Rec. change to SCC* due to increased abundance		
Large Copper Butterfly	Lycaena dispar	Rec. change to SCC* due to extinction in UK		
Adonis Blue	Lysandra bellargus	Rec. change to SCC* due to increased abundance		
Large Blue	Maculinea arion	Re-introductions in progress due to local extinction		
Heath Fritillary	Mellicta athalia			
Silver-studded Blue	Plebejus argus			
*Species of Conservation Concern		<i>UK BAP, 6/1/2007 and Fox et al., 2007</i>		

3.3. CONSERVATION

<u>3.3.1. Value</u>

There are many reasons why butterflies deserve thorough attention for conservation. Like most organisms, butterflies are connected to other organisms in numerous ecosystems across the globe. As larvae, butterflies feed on their host plants. When the butterflies emerge as adults, they provide a source of food for birds (New, 1997).

One function butterflies play in their ecosystems is pollination for plants (New, 1997). Adult butterflies rarely specialize on particular plants. When an adult feeds on the nectar of one flower and becomes coated in pollen, it could transfer that pollen to the next flower on which it feeds. Pollination can occur only if the two flowers are of the same species.

Having healthy butterfly populations is also important for many reasons other than maintaining ecological balance and diversity. Butterflies have an existence value, which in turn creates economic value (Field and Field, 2002). Many people have become interested in butterfly watching, and a number of books have been published on how to turn backyards into butterfly gardens (e.g. Malloy, 2006; Xerces, 1998). Zoos and natural history museums are developing live butterfly gardens to help educate visitors on the wonders of butterflies. The emergence of butterfly gardens and of butterfly watching as a popular hobby demonstrates that people care about their existence; people enjoy knowing that these beautiful insects occur in nature.

Butterfly conservationists in the United Kingdom have tried to utilize the abundance of private butterfly gardens to collect information and to determine best practices for making gardens attractive to butterflies. The British Butterfly Conservation Society coordinated a national survey of butterflies in private gardens in 1990. Garden owners recorded data on the species of butterflies and nectar plants found in the area. Even though more species were documented in rural gardens, well-managed gardens in urban areas were suitable and beneficial for several species (Vickery, 1995). Even though gardens alone cannot support large numbers or diversity of butterflies, they can have a large conservation value if they provide "stepping stones" between larger, wilder patches of habitat (Vickery, 1995).

This existence value also creates an economic value. Most specimens from butterfly gardens are purchased as larvae or pupae from companies that raise farmed butterflies. For

example, The Butterfly Conservatory at the American Museum of Natural History in New York receives pupae from farms in Costa Rica, Texas, and Florida (AMNH, 2007). Some of these companies are in the United States but small-scale butterfly farming has been successful as community conservation projects in other countries. There are several types of butterfly farming, but one involves placing cages over host plants on which adults have oviposited. When the eggs hatch, the larvae are collected, and when they pupate, the pupae are shipped to gardens around the world.

The Kipepeo Project, started in Kenya in 1993, is an example of a successful, community butterfly farm (Gordon, 2003). Since 2001, Kipepeo (which means "butterfly" in Swahili) has been run by the National Museums of Kenya. Farmers collect and raise larvae from the Arabuko-Sokoke Forest. When the larvae pupate, the Kipepeo Project buys the pupae from the farmers and sells them to butterfly houses in the United States and Europe. From 1994-2001, the community earned over \$130,000, and monitoring data have revealed that no damage has been done to wild butterfly populations. The money earned by the farmers helps offset financial damages incurred by occasional trampling of their crops by elephants and baboons that reside in the forest (Gordon, 2003).

Finally, butterflies provide a unique scientific value. Researchers have used butterflies as focal species to study numerous aspects of biology. Many butterflies involved with mimicry complexes shed light on evolutionary adaptation (e.g. Brower, 1996; Mallet and Joron, 1999); others provide examples of sexual selection (e.g. Andersson, 2000; Singer, 1982). Butterflies also have been recognized as an environmental indicator in some areas. As such, they are the focus of studies on the effects of pesticides and pollutants on entire ecosystems (e.g. Dover, 1997; Longley and Sotherton, 1997).

3.3.2. Current Strategies

Currently, diverse strategies are helping to conserve butterfly populations. On a landscape scale, habitat protection and restoration are extremely important, particularly in an era of suburban sprawl that is destroying natural habitat far too quickly. Different species of butterflies occur in different habitats, so general protection of open space that allows the growth of wildflowers and a diversity of potential host plants can provide necessary habitat for butterfly populations to persist. The metapopulation concept has been used to determine which areas of land to preserve (New, 1997). Detailed analyses of existing populations can help predict which unpopulated open spaces might become good habitat for a threatened population if the population had the resources to grow.

Habitat restoration also has been a successful strategy for preserving certain populations of butterflies (e.g. Davies et al. 2005). For example, several species of butterflies occur in open, grassy habitats. In the past, these open habitats were maintained by periodic fires started by natural lightening strikes. However, as these habitats became fragmented by paved roads and housing developments, natural fires have been suppressed. Without fire, the remaining patches of open habitat tend to become overgrown with shrubs and early successional trees. Habitat restoration efforts have focused on returning these overgrown fields to their more natural state, as a result of fire regimes or removal of quick-growing trees, whose shade prevents the flowers and the plants on which butterflies depend from growing (New, 1997).

Another strategy to conserve threatened populations of butterflies is breed-and-release programs. Researchers breed individuals from the threatened population and then reintroduce them to the wild. Either existing populations are supplemented or attempts are made to start new populations by introducing butterflies into previously unoccupied, yet suitable, habitat (e.g.

Martilla et al., 1997). This strategy is sometimes used with restoration projects; once a new area has been restored to the conditions favorable for a particular species of butterfly, individuals will be transplanted from a stable population to the new habitat.

Martilla et al. (1997) documented a successful reintroduction of an endangered butterfly, the Baton Blue, in Southeastern Finland. The Baton Blue naturally occurs in open areas and had lost significant habitat to the overgrowth of pine trees. Researchers chose a location from which the Baton Blue had been extirpated for eight years. They spent two years selectively logging the location in order to make it a more suitable habitat for the butterfly. In 1994, ten females were translocated from a large source population into the newly restored habitat. Two years later, when approximately 50 individuals were counted in surveys, the project was hailed a conservation success by the researchers. However, it was recognized that continued growth of the population was dependent on vigorous management of the land to prevent the pine trees from re-dominating the landscape (Martilla et al., 1997).

Lastly, new policies have aided the conservation of butterflies. In the United States, the Endangered Species Act of 1973 has provided protection for habitat. Listed species are considered in any plans made by federal agencies, and people are prohibited from collecting or selling endangered specimens (Opler, 1995). As of 1997, four species worldwide were listed in Appendix 1 under the Convention on International Trade in Endangered Species (CITES), which prohibits almost all commercial trade of these species (New, 1997). However, in Australia, no butterflies were listed under the Endangered Species Protection Act of 1993 (New, 1997). Other countries, such as Austria and Japan, also provide various levels of protection for threatened species.

4. Effects of climate change on butterflies

Climate changes are expected to have numerous and significant effects on butterfly populations around the world (Parmesan, 1999). In fact, research over the past decades has recorded changes already taking place in various butterfly populations (e.g. Wilson et al., 2005; Beaumont, 2002). Other research focuses on predictive modeling in an attempt to forecast the impending changes (e.g. Crozier and Dwyer, 2006), perhaps in hope that conservationists will be more adept at adjusting existing management plans to consider climate changes in their strategies.

Effects of climate changes on specific species of butterflies include changes in geographic range, in size of range, in seasonal patterns of their life cycles, and in their ecological interactions with other organisms (Hellmann, 2002). There are also cases where climate change is affecting the numbers of species in some habitats. For example, as spring temperatures have increased in Canada, an increase in butterfly richness has been observed (White and Kerr, 2006).

Changes in geographic range and range size are often connected. The best-documented effect of climate change on butterfly populations is a shift in geographic range. Generally, it is expected that, as the climate warms, species will shift to cooler areas, towards higher latitudes (northward in the northern hemisphere where most research has been conducted) or altitudes. The overall size of a species' range depends on the effects of climate on all boundaries. If the northern boundary of a population shifts north at the same speed that the southern boundary shifts, then no change in the size of the range will occur. However, if individuals abandon southern boundary habitats faster than the population shifts northwards, then a contraction of the range will result (Parmesan, 1999).

Conversely, if the northern populations spread faster than southern populations disappear, a range expansion will occur, at least in the short term. So far, more research to date has focused on expansion of the northern or high-elevation boundaries of certain species than on the recession of the southern or low-elevation boundaries (Franco, 2006). Of 35 species studied in Europe, 63% had shifted their ranges north, compared with only 3% that had shifted south (Parmesan, 1999). Parmesan (1999) suggested that the more southerly species exist in more mountainous regions. These species possibly have shifted higher in elevation, even if that resulted in moving southward. However, one study has shown that three out of four species (two specialists and one generalist) with their southern boundaries in Britain have lost parts of their southern range as the boundary has retreated (Franco, 2006).

Crozier and Dwyer (2006) studied changes in geographic range of the Sachem Skipper, which occurs in the northwestern United States. By creating models to predict the consequences of climate changes, they found that the increase in minimum (winter) temperatures caused more changes than increasing maximum (summer) temperatures. The range of the Sachem Skipper shifted faster when the winter temperatures increased compared to when summer temperatures increased. Their models assumed that the focal species would not have difficulty in dispersing assuming environmental factors were conducive to movement. If a species is only limited by the climate and not by dispersal capability, the species ought to be able to shift its range quickly (Crozier, 2003). While this assumption works for the Sachem Skipper, it is likely that other species that are not as prone to dispersal will have more difficulty in shifting their ranges as climate change eliminates suitable habitat. It is also important to consider the ranges and dispersal capabilities of the host plants on which butterflies depend. These changes could also result in geographic range changes for certain species (Braschler and Hill, 2007).

In the United Kingdom, Hill and Thomas (2002) studied the distribution of 51 species of butterflies and, despite the attention placed on range shifts of certain species, they reported no evidence for "systematic shift" of ranges northward. Northward shifts only were applied to 11 out of 46 species, almost all of which have high dispersal capabilities and are habitat generalists. However, species in both northern and southern areas of the United Kingdom have shown shifts to higher elevations. Species in the north have been more likely to become extirpated at the lower boundaries in elevation. In general, species in the north are less mobile than those in the south (Hill and Thomas, 2002).

As migratory species begin to spread to new regions, butterfly biodiversity will increase in some areas. In a monitoring study from 1982 to 2005 in southern England, the number of species of butterflies observed each season increased by 1.34 species. This increase correlated with temperature rises in the area, leading to the conclusion that, with each 1°C increase in temperature, 14.4 more species were present in southern England (Sparks, 2007). This influx of migratory species could be a cause of concern if they monopolize much needed resources for native, sedentary species that will have a more difficult struggle to disperse further north in England. However, if these new, migratory species are threatened in their native, more southerly habitats, then perhaps their shift to southern England will help their populations survive as they find new resources to exploit.

Some studies have focused on range contractions rather than a shift in range for certain species of butterflies. Wilson et al. (2005) studied sixteen species of butterflies that occur at high elevations in Spain. There was a 1.3°C increase in annual temperature over a thirty year period, and they found that lower elevational boundaries rose an average of 212 meters, while the upper limits of the ranges increased for only a few of the species. The overall range contraction for the

sixteen species decreased the amount of suitable habitat by 34%, and the authors predicted continued decline by 50-80% over the next 100 years (Wilson et al., 2005).

In one of the few studies performed in Australia, Beaumont (2002) documented range contractions in multiple butterfly species. Since Australia is an island, there are fewer possibilities for species to shift their geographic ranges in response to climate changes. Even if individuals disperse to cooler environments closer to the pole, there is a limit to how far individuals can move. If individuals abandon the northern, hotter boundaries, the overall range size will contract.

Climate change also will affect butterflies by altering timing of the life cycle, which in turn could disrupt the ecological relationships certain species have with particular plants (McCarty, 2001). All butterflies have evolved certain relationships to other species in their habitats. Larvae depend on host plants to be available at a certain time of year, and adults depend on nectar species on which to feed once they emerge (Menzel & Sparks, 2006). In turn, insect-pollinated plants require that insects feed from their flowers in order to pollinate other plants. A change in timing in one of these species can cause detrimental effects on the other species with which it has an ecological relationship (Root, 2003).

Examples of this de-synchronization in timing already have been documented. In the Netherlands, it was found that certain plants were beginning their growing season a full two weeks earlier than they had historically. Meanwhile, local butterfly species had advanced their flight period by only three days (Wallisdevries and Van Swaay, 2006).

Both observed and modeled studies on butterflies in England support the prediction that butterflies will advance the date of first flight in the spring as the climate warms. One model showed that an increase of 3°C would make butterflies emerge two to three weeks earlier in the

spring (Sparks and Carey, 1995). Observations showed that when spring temperatures increased by 1.5° C in the twentieth century, 13 out of 35 butterfly species advanced their first emergence 17.5 - 36.3 days earlier (Roy and Sparks, 2000). Even though there is a risk that when butterflies change when they first emerge in the spring, they will be de-synchronized with other species in their habitat, an earlier and prolonged flight period could lead to more generations per year – a positive benefit from the effects from climate change (Roy and Sparks, 2000).

Flight dates as much as 24 days earlier in the spring have been recorded for butterflies in lowland California. Forister (2003) claims that the increase in winter temperatures and decrease in rainfall over 31 years led to earlier emergence. More rain in a climate means increased cloudiness and fog, which would discourage emergence of adult butterflies, who benefit from sunny, dry weather (Forister, 2003).

The close relationship between butterflies and their larval host plants has been well recorded. For specialists, habitat is usually limited to areas inhabited by the host plant. In North Wales, *Goneptayx rhamni* (L.), a mobile butterfly species that specializes on two host plants, was shown to shift its range when the host plants were spread to new areas outside of the previous range of the butterfly (Gutierrez and Thomas, 2000). In experimental research involving transplants of individual butterflies in Great Britain, the Brown Argus butterfly (*Aricia agestis*) shifted its preference for a host plant to a species that had occurred only in areas too cold for the butterfly (Thomas et al., 2001).

Experimental research in Switzerland has shown how elevated levels of CO_2 can have a direct effect on butterflies and their host plants. One study that included five species of vital nectar plants for butterflies found that increased CO_2 caused a 40-50% reduction of nectar per flower and a reduction in the percentage of nectar sugar in the nectar mixture. Increased CO_2

also caused one species to flower one week earlier than under normal conditions (Rusterholz, 1998). A reduction in nectar could cause adult butterflies to spend more of their time in search of food rather than on other important behaviors for proliferation of the species, like mating or ovipositing. Another greenhouse experiment, also in Switzerland, found that larvae for one species of butterfly, *Coenonympha pamphilus*, changed its preference for host plant when exposed to elevated CO₂ levels. The development time for the larvae also increased by two days, which possibly could lead to higher risk of predation on the larvae (Goverde, 2003).

Another important consideration is whether the butterfly species overwinters as pupae or larvae. Pupae would be more likely to alter the timing of emergence since larvae are more dependent on being synchronized with their host plants to feed (Forister, 2003). However, even if they overwinter as pupae, adult butterflies still need nectar species when they emerge.

5. Case studies

5.1. POLYGONIA C-ALBUM AND THE SILVER-SPOTTED SKIPPER; UNITED KINGDOM

Some species of butterflies are expected to benefit from impending climate changes. In fact, one study that associated several weather variables with abundance data for multiple species of butterflies in the United Kingdom concluded that predicted climate changes would cause increases in almost all species due to the increase of suitable habitat (Roy, 2001). Those that are capable of high dispersal and of taking advantage of multiple species of host plants and nectar species might respond well to increased temperatures (Crozier, 2003). Even with these traits, a species needs to have access to available habitat if shifting its range will help increase its population. For example, even a species with these characteristics will not benefit if its current range already includes the cooler boundary of an island, such as southern Australia.

The United Kingdom has had a long history of monitoring and documenting the status of its native species of butterflies. These initiatives have paid off, and researchers have observed positive effects of recent climate changes on two species: Polygonia c-album and the Silverspotted skipper (Hesperia comma). Polygonia c-album has expanded its range in Britain more than any other species (Asher, 2001). Braschler and Hill (2007) claim that P. c-album was able to feed on new host plants as individuals dispersed into previously unoccupied habitats. Numerous characteristics of P. c-album are attributed for how this species has been able to adapt so well to new areas, such as hibernating over the winter as pupae, rather than larvae (Warren, 2001). When they emerge as adults, they only need to find nectar species immediately rather than a host plant on which larvae need to feed. P. c-album also is a "mobile generalist", which means it can survive on many different host plants (Braschler and Hill, 2007). Unfortunately, species that are mobile generalists and are more likely to benefit from climate change are also likely to have low conservation value (Braschler and Hill, 2007). If mobile generalists benefit from climate change but specialists suffer, the proportion of generalists to specialists will increase (Menendez, 2006).

Another species in the United Kingdom, the Silver-spotted Skipper, has been hailed a conservation success. The Silver-spotted Skipper was listed as a priority species under the UK Biodiversity Action Plan, and over the period from 1982 to 2000, significant increases in population were documented. The population resurgence has been attributed to a variety of factors, one of which is climate change (Davies et al., 2005). Increased temperatures provided an increase in suitable habitat for the species, particularly at its northern range, which typically has been cooler (Davies et al., 2006). Eggs of the Silver-spotted Skipper are laid on a single plant species, *F. ovina* (Davies et al., 2005). The available habitat for the Silver-spotted Skipper

doubled and its range is currently three times its size from 1982; these increases have been attributed to climate warming, along with intentional habitat management (Pimm, 2001).

5.2. KARNER BLUE BUTTERFLY; UNITED STATES

The Karner Blue butterfly (*Lycaeides melissa samuelis*) is a small, blue butterfly in the Lycaenid family of Lepidoptera. It is a sub-species and the larvae are dependent on Blue Lupine (*Lupinus perennis*) as its sole source of food before pupating. Blue Lupine is a shade-intolerant species and persists only in habitats exposed to regular disturbances that result in bare soil and few tall trees. The Karner Blue used to range from Maine to Minnesota; however, its current natural distribution is restricted to isolated patches in New York, Indiana, Michigan, Minnesota, and Wisconsin. Ohio and New Hampshire have begun reintroduction programs in the last five years (O'Brien, pers. comm.)

The Karner Blue has been listed as federally endangered since 1992 (US FWS, 1992). The Karner Blue also was listed as endangered in the state of New York where populations have declined by over 90% (Schweitzer, 1994). While the New York State Department of Environmental Conservation has monitored populations in key areas since the butterfly was listed as endangered, several organizations, including The Nature Conservancy, have helped with large-scale monitoring projects of all major recovery areas since 1994. Monitoring includes annual sampling counts during the flight season on both private and public lands.

The Karner Blue has two broods each year. Larvae hatch from eggs that have overwintered and begin feeding on Blue Lupine in mid-April. In late May, the larvae form pupae, and seven to eleven days later, the adult butterflies emerge, usually with males emerging a few days earlier than females. Since each individual usually lives only four or five days, the

whole population does not fly at the same time (US FWS, 2003). Over three to four weeks, the number of adults in flight increases, peaks, and then drops to close to zero by late June.

The females from the first brood lay eggs on the Blue Lupine, and five to ten days later, these eggs hatch and the larvae for the second brood feed throughout the month of June to early July. These larvae will pupate and emerge as adults during the month of July. Flight numbers for the second brood are significantly larger than for the first brood since there is decreased mortality of the eggs that have to survive only one or two weeks. When adults from the second brood lay eggs, these eggs have to survive for several months through harsh winters and have to depend on new lupine in the spring when they hatch, all of which causes significant mortality (Schweitzer, 1994; Maxwell and Givnsh, 1995).

Land use alteration has caused a large decline in useable habitat for Karner Blues in New York. The Sandplains used to be open savannah with pitch pines, most likely maintained by natural fires and droughts (Slack, 2002). However, with increased development, the frequency of these disturbances has decreased, allowing larger trees to grow and shade out the shadeintolerant host plant. Development also has caused fragmentation and decreased connectivity between individual patches of suitable habitat. Other recorded threats to the remaining butterfly populations include pesticides, invasive species, and low quantities of nectar for adults (Slack, 2002).

In the summer of 2006, annual sampling revealed decreased numbers across most sites in the Saratoga Sandplains, located in upstate New York. Despite the lack of rigorous scientific research, it was hypothesized that weather patterns were responsible for the decline. There had not been any major changes or declines in suitable habitat in the previous year. Local researchers suggested that increased mortality of eggs during the winter could have caused the decline. It is

thought that significant snow cover is vital to protect the eggs through the winter (O'Brien, pers. comm.), and the winter of 2005-2006 was extremely mild and had heavy rain.

There also was increased rainfall in the spring. In June 2006, New York experienced record amounts of rainfall and temperatures were below normal. It is unclear whether these conditions actually caused increased mortality of adults during the first brood, or if it only decreased the amount of time butterflies spent actively flying around their habitat. It is also possible that decreased activity would lead to a decrease in reproduction, leading to lower numbers in future broods.

According to the National Weather Database, in the winter of 2005-2006, only 30.2 inches of snow fell in Albany, New York – just 50.5% of the average 59.7 inches that usually fall each winter. During the three months from April to June 2006, 18.74 inches of rain fell, 8.24 inches above the average. The amount of rainfall just in June caused the wettest June on record since 1862, with a total of 8.74 inches, 5 inches more than average (Wiley, 2006).

The Karner Blue provides an excellent example of an endangered species that is likely being affected by climate changes, and yet we risk the species going extinct before we even can document these effects. While resources are being spent on habitat restoration for the Karner Blue, consideration of these effects might guide, and perhaps alter, current conservation plans. Even with an abundance of restored habitat, the Karner Blue will not persist if the eggs cannot survive mild winters in the area.

6. Recommendations for future conservation

Although some recent efforts to conserve butterflies are proving to be successful, such as in the examples from the United Kingdom described above, incorporating additional strategies

into current conservation plans could help thwart pending extinctions predicted to occur because of climate change in the next century. Actions include local efforts to preserve open space suitable for butterflies including potential suitable habitat, even if, currently, that space is not conducive for butterflies. Additional research is desperately needed on butterfly species occurring outside of the United States and the United Kingdom. Currently, we can only postulate how climate change could affect current strategies for conservation in other regions, such as Africa or the Neotropics. Finally, global coordination to reduce the CO₂ emissions that are causing rapid climate change in the first place is vital.

The primary reason biodiversity is being lost and natural resources are being decimated is the destruction of natural habitat. As human population has grown exponentially, the amount of land that has not been affected by human presence has decreased enormously. In response, conservation efforts in the last decades have focused on habitat protection. Protection can be in the form of national parks designated by governments or private preserves of land bought by a nonprofit. Often, the occurrence of threatened, endangered, and flagship species makes an area a priority for receiving protection status. In the United States, if a listed, endangered species occurs on a tract of land, then urban development is often prohibited.

While habitat protection has been critical in preserving open space, in the face of climate change, we need to broaden how areas are prioritized. First, just because a currently listed, endangered species does not occur on a piece of property does not mean that that land will not be critical habitat in the future (Crozier, 2003). As the climate warms, butterflies will disperse to new areas that were previously beyond their range. Also, as the climate fluctuates, it is expected that we will experience more extremes in weather. In order to preserve diversity of species, we

need to assure a diversity of habitats so organisms have options for survival depending on different weather conditions (Davies and Wilson, 2005).

Sometimes, suitable habitat for butterflies is defined by the presence of the host plants on which butterflies depend. Even if the habitat patch is un-colonized by butterflies, the area could be protected because it might be colonized in the future. While basing conservation on metapopulation theory is a good start, it is important also to recognize that the distribution of host plants might be affected by climate change. Therefore, patches void of vital host plants might become populated as the climate warms (Braschler and Hill, 2007). Also, butterflies might be able to adapt to feed on new species of host plants, deeming new patches suitable for preserving butterflies. Although using the distribution of host plants can help to guide conservation efforts, habitat that currently has no butterflies and no host plants still might become important open space in the future as the distributions of organisms shift in response to global changes.

In general, intensive conservation of natural habitat will be crucial to the proliferation of butterflies as they and the plants on which they depend for survival adapt to the changes in their environments. If we continue our strategy of protecting only the habitat where an endangered species exists now, in a few decades, those individuals will disappear. However, if we can be proactive in the face of climate change and recognize the importance of all remaining open space, we might be able to provide enough diversity to aid organisms in adapting to these changes. Even as some species have adjusted by shifting their ranges, suitable habitat is still in decline. In Britain, where climate warming is being heralded for helping some species recover, overall, only 50% of mobile-generalists have increased their ranges, while up to 89% of specialists have decreasing ranges (Warren, 2001).

An increase in experimental introductions could help keep population numbers high for species threatened by climate change. Even if suitable habitat with an abundance of host plants has been protected, individuals of certain species might not be able to populate the patch if they have low dispersal capability. Reintroductions from captive-bred populations or transplanted individuals from other, colonized populations might allow those species to take advantage of additional habitat (Davies and Wilson, 2005).

Another type of habitat that could be increased is private, "backyard" gardens, filled with native nectar species and host plants for multiple species of butterflies. Even managed landscapes with exotic species can help butterfly populations move along corridors to larger habitat patches. A study in Costa Rica showed that many butterflies that occur in forests used heavily managed botanical gardens outside of their natural habitat (Daily and Ehrlich, 1995). Public campaigns to encourage the construction of butterfly gardens on private land also provide a forum for increasing public awareness and education about butterflies and an outlet for the general public to participate in and benefit from conservation efforts.

More research is needed if we want to be able to incorporate predicted effects of climate change into conservation planning for the preservation of endangered butterflies (Root, 2003). We need more information on how butterflies might adapt to changes, on how host plants and nectar species might be affected, and on how de-synchronization between butterflies and other aspects of their ecosystems will cause danger for their survival. It also is necessary to study species outside of northern, temperate zones. Thousands of unstudied species occur in the tropics and may also be affected by climate change. However, so far, we have no documentation on what these changes might be. Conservationists working in the tropics cannot integrate scientific

predictions of the effects of climate change into conservation plans if there is no research on what these effects will be.

Finally, current efforts to decrease the concentration of CO₂ in the atmosphere must be pursued actively by the global community. If everyone takes action now, we ought to be able to avoid worst-case scenarios. International agreements need to be signed, and governments need to be held accountable for their commitments. Businesses need to initiate research for clean, affordable technologies. Individuals need to recognize the importance of decreased consumption of carbon-emitting resources. Only through global cooperation will everyone continue to benefit from the continued existence of the Baton Blue, the Regal Fritillary, the Silver-spotted Skipper, and the Karner Blue.

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8. References

AMNH. 2007. American Museum of Natural History. New York. http://www.amnh.org/exhibitions/butterflies/highlights/conservation.php. Date accessed: 29 June 2007.

Andersson, J., A. K. Borg-Karlson, and C. Wiklund. 2000. Sexual cooperation and conflict in butterflies: a male-transferred anti-aphrodisiac reduces harassment of recently mated females. Proceedings of the Royal Society of London Series B 267(1450): 1271-1275.

Arnold, R. A. 1983. Ecological studies of six endangered butterflies (Lepidoptera, Lycaenidae): island biogeography, patch dynamics, and the design of habitat preserves. University of California Press, Berkeley.

Asher, J. M. Warren, R. Fox, P. Harding, G. Jeffcoate and S. Jeffcoate. 2001. The Millenium Atlas of Butterflies in Britain and Ireland. Oxford University Press, Oxford.

Beaumont, L. J. and L. Hughes. 2002. Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. Global Change Biology 8, 954-971.

Braschler, B. and J. K. Hill. 2007. Role of larval host plants in the climate-driven range expansion of the butterfly *Polygonia c-album*. Journal of Animal Ecology 76, 415-423.

Brower, A.V. Z. 1996. Parallel race formation and the evolution of mimicry in *Heliconius* butterflies: a phylogenetic hypothesis from mitochondrial DNA sequences. Evolution 50(1): 195-221.

Crozier, L. 2003. Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopedes campestris*. Oecologia 135:648-656.

Crozier, L., and G. Dwyer. 2006. Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. American Naturalist 167:853-866.

Daily, G. C. and P. R. Ehrlich. 1995. Preservation of biodiversity in small rain-forest patches – rapid evaluations using butterfly trapping. Biodiversity and Conservation 4 (1): 35-55.

Davies, Z. G., R. J. Wilson, T. M. Brereton, and C. D. Thomas. 2005. The re-expansion and improving status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain: a metapopulation success story. Biological Conservation 124: 189-198.

Davies, Z.G., R. J. Wilson, S. Coles, and C. D. Thomas. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. Journal of Animal Ecology 75: 247-256.

Dennis, R. L. H. 1993. Butterflies and Climate Change. Manchester University Press, Manchester.

Dover, J. W. 1997. Conservation headlands: effects on butterfly distribution and behaviour. Agriculture Ecosystems and Environment 63(1): 31-39.

Field, B. C. and M. K. Field. 2002. Environmental economics: an introduction. McGraw-Hill Irwin, Boston.

Forister, M. L., and A. M. Shapiro. 2003. Climatic trends and advancing spring flight of butterflies in lowland California. Global Change Biology 9:1130-1135.

Fox, R., M. S. Warren, J. Asher, T. M. Brereton, and D. B. Roy. 2007. The state of Britain's butterflies 2007. Butterfly Conservation and the Centre for Ecology and Hydrology, Wareham, Dorset.

Franco, A. M. A., J. K. Hill, C. Kitschke, Y. C. Collingham, D. B. Roy, R. Fox, B. Huntley, and C. D. Thomas. 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. Global Change Biology 12:1545-1553.

Gilpin, M.E. and Hanski, I. 1991. Metapopulation Dynamics: empirical and theoretical investigations. Academic Press, London.

Gordon, I. 2003. Harnessing butterfly biodiversity for improving livelihoods and forest conservation: the Kipipeo Project. Journal of Environment and Development.

Goverde, M., and A. Erhardt. 2003. Effects of elevated CO2 on development and larval foodplant preference in the butterfly *Coenonympha pamphilus* (Lepidoptera, Satyridae). Global Change Biology 9:74-83.

Gutierrez, D., and C. D. Thomas. 2000. Marginal range expansion in a host-limited butterfly species *Gonepteryx rhamni*. Ecological Entomology 25: 165-170.

Haddad, N.M. 1999. Corridor use predicted from behaviors at habitat boundaries. The American Naturalist, 153(2): 215-227.

Hellmann, J. J. 2002. "Butterflies as model systems for understanding and predicting the biological effects of climatic change" in Wildlife responses to climate change. S. H. Schneider and T. L. Root, eds. Island Press, Washington, D.C. pp. 93-126.

Hill, J. K., C. D. Thomas, R. Fox, M. G. Telfer, S. G. Wilis, J. Asher, and B. Huntley. 2002. Responses of Butterflies to Twentieth Century Climate Warming: Implications for Future Ranges. Proceedings of the Royal Society of London B 269(1505): 2163-2171.

Hoyle, M., and M. James. 2005. Global warming, human population pressure, and viability of the world's smallest butterfly. Conservation Biology 19:1113-1124.

[IPCC] Intergovernmental Panel on Climate Change. 2001. Climate change : the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Eds. J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell and C. A. Johnson. University Press, Cambridge.

Larsen, T. B. 1995. "Butterfly biodiversity and conservation in the Afrotropical region" in in Ecology and Conservation of Butterflies, ed. A. S. Pullin. Chapman & Hall, London.

Levins. R. 1970. Extinction. Pages 77-100 in M. Getstenhaber, editor. Some mathematical problems in biology. American Mathematical Society, Providence. Rhode Island.

Longley, M. and N. W. Sotherton. 1997. Factors determining the effects of pesticides upon butterflies inhabiting arable farmland. Agriculture Ecosystems and Environment 61(1): 1-12.

Mallet, J. and M. Joron. 1999. Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance, and speciation. Annual Review of Ecology and Systematics 30: 201-233.

Malloy, M. 2006. Butterfly gardening made easy for southwest Florida. BookSurge Publishing.

Marttila, O., K. Saarinen, and J. Jantunen. 1997. Habitat restoration and a successful reintroduction of the endangered Baton Blue butterfly (*Pseudophilotes baton schiffermuelleri*) in SE Finland. Annales Zoologici Fennici 34: 177-185.

Maxwell, J. and T. Givnish, 1994. Research on the Karner blue butterfly at Fort McCoy, Wisconsin: Progress report for the 1993 field season. Report to the US Fish and Wildlife Service and US Department of Defense, December 1993.

McCarty, J. P. 2001. Review: Ecological consequences of recent climate change. Conservation Biology 15(2): 320-331.

Menendez, R., A. G. Megias, J. K. Hill, B. Braschler, S. G. Willis, Y. Collingham, R. Fox, D. B. Roy, and C. D. Thomas. 2006. Species richness changes lag behind climate change. Proceedings of the Royal Society B 273: 1465-1470.

Menzel, A., T. H. Sparks, N. Estrella and D. B. Roy. 2006. Altered geographic and temporal variability in phenology in response to climate change. Global Ecology and Biogeography 15: 498-504.

New, T. R. 1997. Butterfly Conservation. 2nd ed. Oxford University Press, Melbourne.

O'Brien, Kathy. 2006. Personal Communication. Wildlife Biologist. New York State Department of Environmental Conservation – Endangered Species Unit; Albany, New York.

Opler, P. A. 1995. "Conservation and management of butterfly diversity in North America" in Ecology and Conservation of Butterflies, ed. A. S. Pullin. Chapman & Hall, London.

Parmesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. J. Tennent, J. A. Thomas, and M. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579-583.

Pimm, S. L. 2001. Entrepreneurial insects. Nature 411:531-532.

Pollard, E. and T. J. Yates. 1993. Monitoring butterflies for ecology and conservation. Chaman & Hall, London.

Pyle, R. M. 1981. The Audubon Society Field Guide to North American Butterflies. Alfred A. Knopf, New York.

Ries, L. and D. M. Debinski. 2001. Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. Journal of Animal Ecology, 70: 840-852.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421: 57-60.

Root, T. L., and S. H. Scheider. 2002. "Climate change: overview and implications for wildlife" in Wildlife responses to climate change. S. H. Schneider and T. L. Root, eds. Island Press, Washington, D.C. pp. 1-56.

Roy, D. B., and T. H. Sparks. 2000. Phenology of British butterflies and climate change. Global Change Biology 6:407-416.

Rusterholz, H. P., and A. Erhardt. 1998. Effects of elevated CO2 on flowering phenology and nectar production of nectar plants important for butterflies of calcareous grasslands. Oecologia 113:341-349.

Schweitzer. 1994. Prioritizing Karner blue butterfly habitats for protections activities. In Karner Blue Butterfly: A Symbol of a Vanishing Landscape, edited by David A. Andow, Richard J. Baker, and Cynthia P. Lane – St. Paul: Minnesota Agricultural Experiment Station.

Singer, M. C. 1982. Sexual selection for small size in male butterflies. American Naturalist 119(3): 440-443.

Slack, S. 2002. Saratoga Sandplains Karner Blue Butterfly Habitat Management Plan. Report to The Nature Conservancy: Eastern New York Chapter.

Sparks, T. H., R. L. H. Dennis, P. J. Croxton, and M. Cade. 2007. Increased migration of Lepidoptera linked to climate change. European Journal of Entomology 104: 139-143.

Sparks, T. H. and P. D. Carey. 1995. The responses of species to climate over 2 centuries – an analysis of the Marsham phonological record, 1736-1947. Journal of Ecology 83(2): 321-329.

Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Mushche, and L. Conradt. 2001. Ecological and evolutionary processes at expanding range margins. Nature 411:577-581.

[UK BAP] United Kingdom Biodiversity Action Plans. http://www.ukbap.org.uk. Accessed: 1 June 2007.

[US FWS] United States Fish and Wildlife Service. Threatened and Endangered Species System (TESS). http://ecos.fws.gov/tess_public. Accessed: 1 June 2007.

[US FWS] United States Fish and Wildlife Service. 2003. Final Recovery Plan for the Karner Blue Butterfly (*Lycaeides melissa samuelis*) U.S. Fish and Wildlife Service, Fort Snelling, MN.

Vickery, M. L. 1995. "Gardens: the neglected habitat" in Ecology and Conservation of Butterflies, ed. A. S. Pullin. Chapman & Hall, London.

Wallisdevries, M. F. and C. A. M. Van Swaay. 2006. Global warming and excess nitrogen may induce butterfly decline by microclimate cooling. Global Change Biology 12: 1620-1626.

Warren, M. S., J. K. Hill, J. A. Thomas, J. Asher, R. Fox, B. Huntley, D. B. Roy, M. G. Telfer, S. Jeffcoate, P. Harding, G. Jeffcoate, S. G. Willis, G.-D. J. N., D. Moss, and C. D. Thomas. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414:65-69.

White, P. and J. T. Kerr. 2006. Constrasting spatial and temporal global change impacts on butterfly species richness during the 20th century. Ecography 29: 908-918.

Wiklund, C. and C. Ahrberg. 1978. Host plants, nectar source plants, and habitat selection of males and females of *Anthocharis cardamines* (Lepidoptera). Oikos 31(2): 169-183.

Wiley, A. S. 2006. Karner Blue Butterfly (*Lycaeides melissa samuelis*) Population Monitoring Results – 2006 for the Saratoga Sandplains Recovery Unit. Report to the NYS Department of Environmental Conservation – Endangered Species Unit.

Wilson, R. J., D. Gutierrez, J. Gutierrez, D. Martinez, R. Agudo, and V. J. Monserrat. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. Ecology Letters 8: 1138-1146.

Xerces Society and Smithsonian Institution. 1998. Butterfly Gardening: creating summer magic in your garden. Sierra Club Books.