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Source: The Journal of the Lepidopterists' Society, 65(2) : 119-125

Published By: The Lepidopterists' Society

URL: https://doi.org/10.18473/lepi.v65i2.a4

Journal of the Lepidopterists' Society
65(2), 2011, 119–125

THE ROLE OF ENVIRONMENTAL FACTORS IN THE NORTHEASTERN RANGE EXPANSION OF *PAPILIO CRESPHONTES* CRAMER (PAPILIONIDAE)

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ABSTRACT. The Giant Swallowtail butterfly, *Papilio cresphontes* Cramer (Papilionidae), has been reported in New York State for nearly 150 years. In recent years there has been an unexplained increase in *P. cresphontes* occurrences along the northeastern periphery of its geographical range. This study examined historical records to describe the movement of *P. cresphontes* populations into New York State and adjacent Ontario. Climate data and field studies were used to identify environmental factors that may influence the range expansion, which was found to correspond with an absence of September frosts beginning in 2001. Field studies indicated that some *P. cresphontes* larvae were capable of withstanding multiple frosts and descended to pupate normally into late October in the range expansion area. Although the larvae may have adapted to endure cooler temperatures to some degree, the effects of warming temperatures on other factors such as natural enemies and larval host plant quality in autumn may influence the spread of *P. cresphontes* populations at least as much as larval frost tolerance.

Additional key words: Butterfly range expansion, climate change, biogeography

In 1864 the first record of a Giant Swallowtail (*Papilio cresphontes* Cramer, Papilionidae) was documented for the state of New York (Scudder 1889; Lintner 1893; Comstock & Comstock 1929), but over the last century sightings of this butterfly have been extremely scarce until the past nine years (New York State Butterfly Records 2001–2005; Dirig 2008, 2009). Indeed, over the past decade *P. cresphontes* has become increasingly abundant in central New York State and appears to be expanding along the northeastern boundary of its range. The causes and characteristics of this recent increase in geographical distribution and population density of *P. cresphontes* are currently unknown.

This paper provides some of the first field data on the presence and survival of *P. cresphontes* in central New York, and the influence of environmental factors on the range expansion of this butterfly. We followed a *P. cresphontes* larval field population to pupation, assessing their ability to overwinter in the area and their vulnerability to natural enemies. Weather records were used to examine climatic impacts on larval populations, and literature and historical records revealed distribution and occurrence reports of *P. cresphontes*. These data suggest that what shapes the geographical distribution of *P. cresphontes* may not just be host plant abundance, available habitat, or freeze-induced mortality as previously emphasized (Scudder 1889; Wild 1939; Tyler et al. 1994; Hughes 2000; Dennis et al. 2005; Hellman et al. 2008), but may well include the effect of climate on host plant condition and abundance of parasitoids.

METHODS

Field studies. The main field site for this autumn 2008 study was Cornell University's Eames Memorial Natural Area, part of Mud Creek Swamp, located near Freeville, New York, approximately 20 km northeast of Ithaca. The area covers 11 ha and was selected based on previous sightings of *P. cresphontes*, an abundance of the local host plant (*Zanthoxylum americanum* Mill., Rutaceae), and prior evidence of larval populations. In October and November, foliage of *Z. americanum* was searched for the presence of *P. cresphontes* larvae and pupae. Each tree with one or more larvae was marked with flagging tape, and trees with larvae were revisited later for pupal searches.

After winter passed, marked *Z. americanum* were thoroughly checked for pupae. Because *P. cresphontes* larvae generally pupate within 5 m of their host plant (West & Hazel 1996), all vegetation within a 5 m radius of the host plant was exhaustively checked for pupae. This was used as a standardized searching method. Cadavers of *P. cresphontes* collected from the site were inspected for evidence of predation, parasitoids or other sources of mortality by Dr. Ann Hajek at Cornell University.

Distribution studies. Occurrence reports of *P. cresphontes* in the region were compiled from annual Season Summaries in News of the Lepidopterists' Society (1947–2008) and New York State Butterfly Records (2001–2005). Ontario occurrence reports were gathered from Season Summaries in News of the Lepidopterists' Society (1970–2008) as well as summaries published by the Toronto Entomologists' Association between 1977 and 2002. Many occurrence records were documented by the same person at each town or county, suggesting there was consistency in the reports and sampling efforts. Although it is impossible to completely disregard an increase in sampling, *P. cresphontes* is such a large, conspicuous, and somewhat rare butterfly that it is expected to be reported if it occurred in any numbers. The information gathered from these reports was used to create graphs and a map tracking the movement of *P. cresphontes* into New York. A one-tailed two-sample unequal variance *t*-test was run to examine the differences in number of *P. cresphontes* occurrences over time, and means were derived from annual occurrences.

Weather data. To determine if climate change had an impact on *P. cresphontes* populations, New York weather records from 1980–2008 were obtained from the Northeast Regional Climate Center (NRCC 2009). Only frosts from the Ithaca, New York weather station were used in data analysis. Every frost event, i.e., temperature occurrence of 0° C or colder, between the months of September and November (the time period when larvae can still be found feeding on host plants) was noted. A two-tailed two-sample unequal variance *t*-test was run to compare frost incidences to *P. cresphontes* occurrences. The occurrences of below-freezing temperatures in autumn 2008 were also compared with the amount of time *P. cresphontes* larvae continued to feed on *Z. americanum*, despite the frigid temperatures. Finally a two-tailed Fisher's exact test was used to examine the association between butterfly occurrences and frost absence. Means were calculated based on annual frost reports for September–November and September only.

RESULTS

Historical records. The season summaries and occurrence reports of *P. cresphontes* in New York showed no official sightings between 1947 and 2000 (there are scarce previous reports of *P. cresphontes* in the state from older historical records, and informal reports support that this species was rare or nonexistent in central New York at least during the 1960's; A. Shapiro, pers. comm.). Beginning in 2001, there was a rapid increase in *P. cresphontes* reports (Fig. 1). There is a significant difference between past (1947–2000) and recent (2001–2008) butterfly occurrences (P = 0.036, DF = 61, past occurrences $\bar{x}$ = 0.0, SE = 0.0; recent occurrences $\bar{x}$ = 6.38, SE = 3.01). Based on recent sightings, it appears that the butterfly populations are moving both north and east through New York (Fig. 2A).

According to the season summaries and sighting reports from Ontario, the first post-1970 observation of *P. cresphontes* was made in 1974. Reports were much more common from 1975–2008 in Ontario than they were in New York. A significant difference is observed between past (1970–2000) and recent (2001–2008) reported *P. cresphontes* occurrences in Ontario, with a much higher number of occurrences during recent years (P = 0.007, DF = 38, past occurrences $\bar{x}$ = 13.65, SE = 2.40; recent occurrences $\bar{x}$ = 99.75, SE = 53.78; see Fig. 1). We recognize a boom and bust pattern during 2005–2008, preceded by no occurrence reports in 2004 and very few in 2002–2003. Multiple Ontario sightings described groups of tens of members, and a 2005 sighting reported 306 *P. cresphontes* adults in one large meadow on Pelee Island in Essex County.

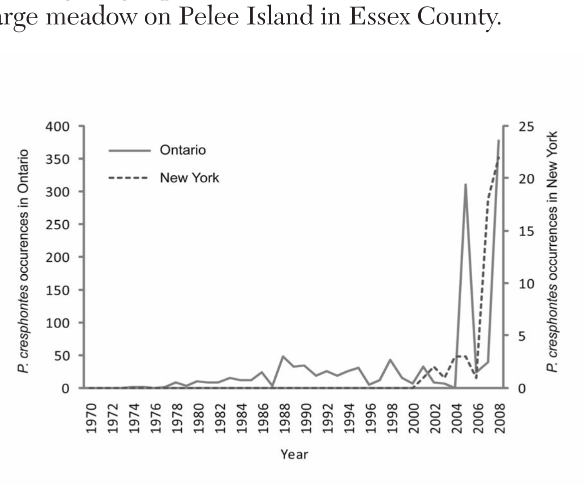

FIG. 1. Combined occurrence reports (larvae and adults) of *P. crephontes* in Ontario and New York State, 1970–2008.

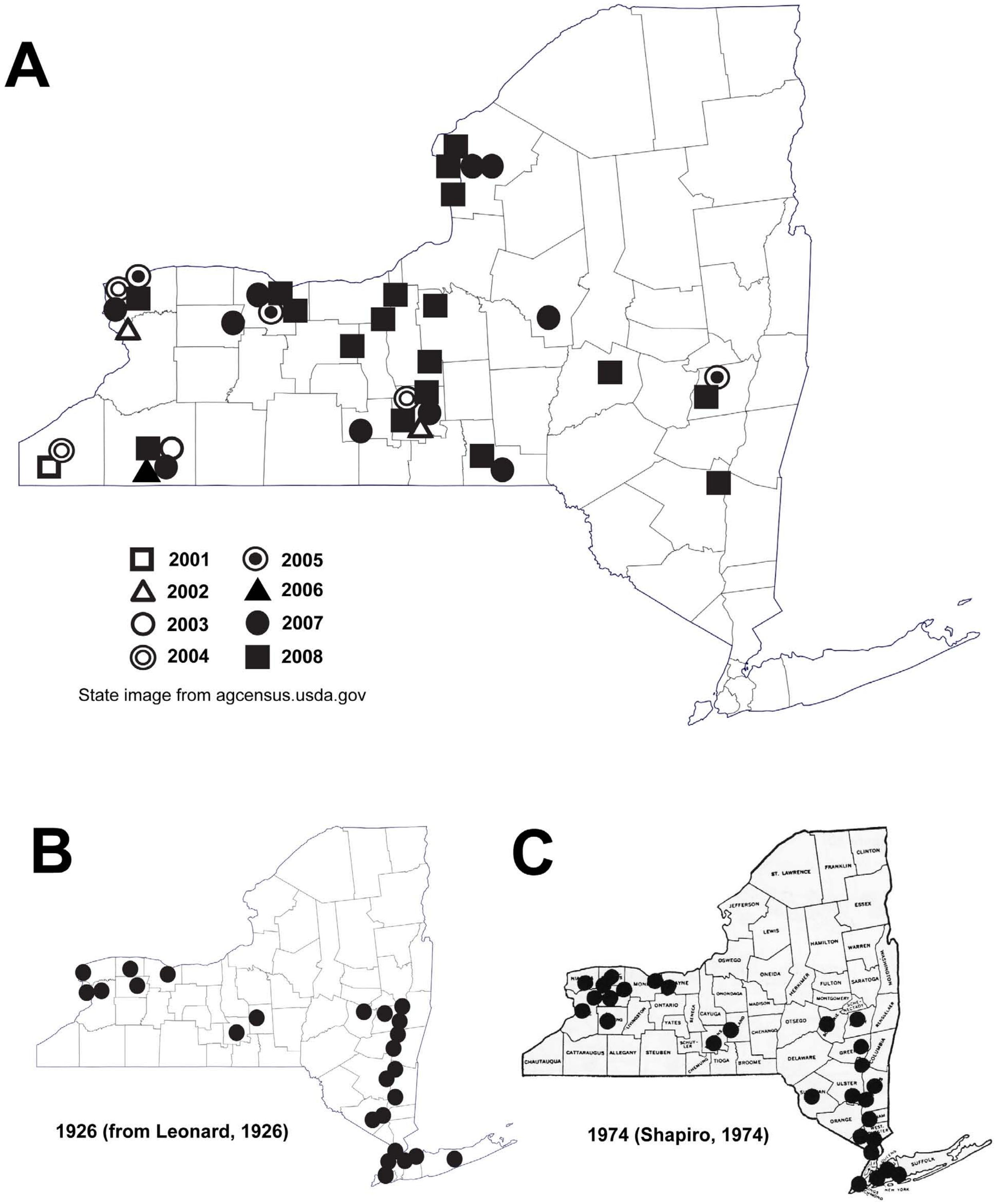

FIG. 2. Recent versus historical distribution of *P. cresphontes* sightings in New York State.

Fall Temperatures. Ithaca frost records from September through November during 1980–2008 showed no statistically significant difference between the total numbers of past (1980–2000) and recent (2001–2008) frost occurrences ($P = 0.127$, $DF = 28$, past occurrences $\bar{x} = 26.0$, $SE = 0.976$; recent occurrences $\bar{x} = 22.5$, $SE = 1.880$). However, no frosts were reported during the month of September in Ithaca after 2000. This also holds true for most of the 33 locations in New York where other sightings occurred. There is a significant difference between past and recent September frost occurrences, with frosts more common prior to 2001 ($P < 0.001$, $DF = 28$; past occurrences $\bar{x} = 0.857$, $SE = 0.199$; recent occurrences $\bar{x} = 0.0$, $SE = 0.0$). The Fisher's exact test shows a significant relationship between the absence of September frosts and the presence of *P. cresphontes* ($P = 0.0089$; Fig. 3). All frost data in general showed the least number of frosts in September and the most in November.

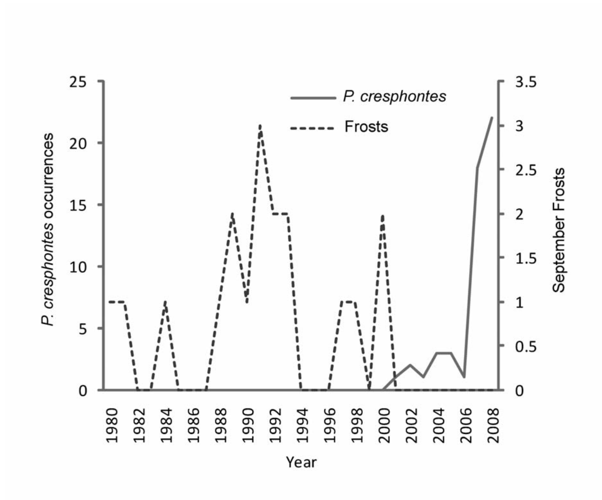

FIG. 3. Occurrence reports of *P. cresphontes* in New York State (1980-2008), compared to September frost records for Ithaca.

Larval survival. Twelve *P. cresphontes* larvae of various instars were found at the Eames field site on 3 October 2008, on five different *Z. americanum* plants. The larvae were monitored over the course of four weeks, during which time there were multiple gaps where the air temperature fell below freezing for several hours each time. All 12 larvae survived the first frost of the season (7 October, minimum temperature; -1.2° C, 6 hours (h) frost duration). Larvae surviving the remaining frosts endured minimum temperatures of -2.7° C, -3.9° C, -0.4° C, -2.5° C, -3.1° C, and -0.9° C, with temperatures below freezing for 6 h, 10 h, 10 h, 10 h, 8 h, and 3 h, respectively. Evidence of mortality was not seen until 19 October, with further mortality observed on 26 October (Table 1). Six larval cadavers were found at the site, the majority of them hanging from the host plant. According to laboratory examination, the cause of mortality of one specimen appeared to be predation. It had a large hole in the dorsum through the body, yet looked very healthy with a gut full of food. The other larvae contained no recognizable evidence of the cause of mortality.

The Eames field site was revisited on 28 March 2009, to search for pupae. Only one *P. cresphontes* specimen was found. It appeared to be a dead pre-pupa; it was partially decomposed, with the head capsule present but split in half. The cadaver was propped in a silken girdle, indicating that this was a pupation attempt. A large cavity was found in the center of the pre-pupa, likely from a parasitoid that exited the larval host.

TABLE 1. Number of *P. cresphontes* larvae over time on five *Z. americanum* host plants at Eames Memorial Natural Area near Ithaca, New York. Larval instars are indicated by the instar number followed by "*i*", preceded (outside of parenthesis) by the number of larvae found at that instar. Frosts (NRCC 2009) were recorded on 7, 18, 19, 20, 21, 23, and 24 October.

	Plant #1		Plant #2		Plant #3		Plant #4		Plant #5	
Date	Living	Dead	Living	Dead	Living	Dead	Living	Dead	Living	Dead
3 Oct 08	1(5*i*)	0	3(3*i*) 2(5*i*)	0	1(3*i*) 1(5*i*)	0	1(3*i*) 1(4*i*) 1(5*i*)	0	1(5*i*)	0
11 Oct 08	1(5*i*)	0	3(3*i*) 2(5*i*)	0	1(3*i*) 1(5*i*)	0	1(3*i*) 1(4*i*) 1(5*i*)	0	1(5*i*)	0
19 Oct 08	1(5*i*)	0	3(3*i*)	2	0	0	2(5*i*)	1	1(5*i*)	0
26 Oct 08	0	0	0	1	0	0	2(5*i*)	1	0	1

DISCUSSION

Larval frost tolerance. The results from the field data indicate *P. cresphontes* larvae are capable of withstanding multiple frosts (as low as -3.9° C) and temperatures below freezing for up to 10 hours. The minimum lethal temperature for *P. cresphontes* larvae is undetermined. Evidence confirming that larvae can endure not one but several frosts contradicts a previous hypothesis about *P. cresphontes* by Scudder (1889) stating that "frosts must here [Massachusetts] as elsewhere kill off the belated caterpillars". He also suggested the progeny of later larval broods would be unable to grow to maturity due to frosts. Hanks (1988) described the lack of giant swallowtail butterfly observations in Ontario later in the season as a probable indication the adult population was killed by cold temperatures.

It is common to link freezing temperatures with insect mortality. In other insect larvae, such as the beetle *Oncideres pustulatus* LeConte (Cerambycidae), freezing was responsible for high mortality rates that likely limit its northern distribution in Texas (Rice 1986). There are several published examples, however, where lepidopterans and other insects (in particular larvae) have been capable of withstanding temperatures below freezing (Sømme 1986; Bale 1991; Storey & Storey 1996; Brown et al. 2004; Ross 2008). Observations by Hine (1908) concerning the effects of freezing on the Cattail borer moth (*Bellura obliqua* Walker, Noctuidae) indicate successful and complete recovery by larvae from multiple freezes ranging from -19 to -28° C. Based on field observations with *P. cresphontes* in October 2008, it is possible this species has recently adapted to endure cold temperatures on the northern periphery of its range.

Frosts affect host plant quality. Although frost data from Ithaca for the past 29 years do not reveal significant changes in the number of frosts each fall, they do indicate a higher frequency of September frosts before the *P. cresphontes* boom. After 2000, no September frosts were recorded. Perhaps *Z. americanum* plants had been previously affected by early frosts before the 21st century enough to starve late larval populations of *P. cresphontes*, or slow their growth rate and in turn increase the likelihood of attacks by natural enemies. If early frosts had a significant impact on plant populations, then they likely had an impact on the herbivores dependent upon those plants.

That climate affects larval populations through poor host quality is supported by other research. The unavailability of fresh food for larvae during late autumn and early winter is one suggestion why subtropical, southern butterflies do not expand into more northern environments (Ross 2008). The caterpillars become so severely weakened by starvation that they die of metabolic failure or prolonged exposure to predators. During a follow-up visit to the field site in late October, the *Z. americanum* host plants were nearly bare and had dropped most of their leaves. Nevertheless, there were still two fifth-instars continuing to feed on the remaining poor-quality leaves. There is a connection made between chill effects, larval growth rate, and vulnerability to predators, the latter two comprising the slower-growth/higher-mortality hypothesis (Feeny 1976; Clancy & Price 1987; Fordyce & Shapiro 2003). Cooler temperatures inhibit the growth rate of larvae, which in turn leads to a greater likelihood of encountering a predator or other natural enemy. This hypothesis coincides well with our field results from the cadavers. With evidence of both parasitism and a predator assault, it seems logical to suspect that natural enemies are affecting the survivorship of *P. cresphontes* larvae in central New York.

Range expansion. Previous hypotheses that butterfly ranges are limited by host distribution (Tyler et al. 1994; Hughes 2000; Dennis et al. 2005) are contradicted by the results. *Z. americanum* is widely distributed throughout the eastern half of North America (USDA Plant Database 2009), and climate likely plays a greater role in range expansion than host plant availability. Other butterfly populations show evidence of distribution shifts due to temperature changes in their natural area (Parmesan et al. 1999). *Papilio zelicaon* Lucas (Papilionidae) and *Erynnis propertius* Scudder (Hesperiidae) may increase at their range edge with warming (Hellmann et al. 2008), and warmer winters drive range expansion in the sachem skipper *Atalopedes campestris* Boisduval (Hesperiidae) (Crozier 2004). Larger fluctuations in butterfly populations are seen in more northern than southern ranges, and temperature most likely has the largest influence on butterflies during late larval and pupal development (Dennis 1993). Co-variations between sites and species further indicate climate could be a major source of population fluctuations. Boom and bust patterns, such as the pattern in Ontario from 2005–2008, are common at geographic range margins where populations expand in warm years but retract during cool years (Thomas et al. 1998). Shapiro (1974) considered *P. cresphontes* likely a breeding resident in western New York and breeding sporadically in the Hudson Valley, and Klots (1951) mentions that this species is sporadic northward. This is a pattern consistent with most species at the northern edge of their range.

Although data support a strong correlation between lack of September frosts and an increase in *P. cresphontes* occurrences, we can only present a plausible causal hypothesis that the decrease in autumn frosts could be responsible for the increase in occurrences. Other environmental variables may contribute to the range expansion in this species, therefore we emphasize that this correlation does not equal causation. There are two instances of three consecutive years without September frosts prior to 2000, yet no sightings were made following these intervals, which further suggests other factors besides (or in addition to) lack of September frosts have contributed to the increase in occurrences and range expansion.

Given the map created using occurrence reports, a distributional shift north and east into New York State is recognized. The individuals observed most recently in central New York may have traveled eastward from the Rochester and Niagara Falls regions, or perhaps crossed into New York from Ontario (assuming higher densities of the species exist in Ontario, as depicted in the occurrence reports). When a historical distribution map (data from Leonard 1926) for *P. cresphontes* is compared to the map created by Shapiro in 1974, the distributions are quite similar (Fig. 2B and 2C). The similarity between the two maps is likely a result of no new records found during the intervening period, and no distinction is made in Shapiro's map between historic and current records. There does not appear to be any significant increase in the range, although the possibility of a decrease prior to 1974 is not excluded. This leads us to believe that population shifts by *P. cresphontes* were rare in New York State between 1926 and 1974, and provides further evidence that colonization and range expansion by this species is a recent phenomenon that requires close monitoring.

Based on field and historical data, an assumption can be made that populations of *P. cresphontes* will continue to appear in central New York and possibly increase in numbers, given the recent trend in heightened occurrences. Their distribution is predicted to expand in a northern and eastern direction toward appropriate habitats where the larval host plant is available, but cooler temperatures and natural enemies may slow the growth of certain populations. Over the course of the past century, *P. cresphontes* larvae may have adapted to endure cooler temperatures, thus allowing the opportunity for the advancement of populations beyond the limits of their previous geographical range. It is unclear why this adaptation would be happening now since the species has such a long history in North America. Further studies investigating the progression of *P. cresphontes* populations through New York will be helpful in connecting factors such as climate change, anthropogenic influences, and natural enemies to fluctuations in butterfly distribution ranges. Details following this movement will present valuable information regarding distributional shifts, not merely in butterflies, but in other organisms that may expand their ranges and colonize this region in future years.

ACKNOWLEDGEMENTS

Thanks to Jeffry Petracca for field assistance and help gathering occurrence reports; Ann Hajek for examining cadavers and providing useful information on parasitoids; Karen Edelstein for aid in fieldwork; Jessica Rennells at the Northeast Regional Climate Center for detailed frost records; Art Shapiro and two anonymous reviewers for manuscript suggestions; Betsy Darlington and Andy Zepp for approving research permits at the Salmon Creek Finger Lakes Land Trust Preserve; The Natural Areas Committee of Cornell Plantations for permission to conduct field work at the Eames Memorial Natural Area; The Comstock Memorial Library for allowing access to the rare book collection; and the Cornell University College of Agriculture and Life Sciences Honors Program for funding this project.

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Received for publication 16 January; revised and accepted 27 December 2010