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Tiger Swallowtail, <u>Papilio canadensis</u> Tiger Swallowtail, Papilio canadensis

presented by

Piera Y. Giroux

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M.S. degree in Entomology

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TESTING THE "COLD POCKET" HYPOTHESIS: OVIPOSITION PREFERENCE IN THE CANADIAN TIGER

SWALLOWTAIL, PAPILIO CANADENSIS

By

Piera Y. Giroux

A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Department of Entomology

ABSTRACT

TESTING THE "COLD POCKET" HYPOTHESIS: OVIPOSITION
PREFERENCES OF THE CANADIAN TIGER SWALLOWTAIL, PAPILIO
CANADENSIS

By

Piera Y. Giroux

Three areas in Northern Michigan; Vanderbilt, Pellston and Cross Village were compared for climate differences; host plant phenology differences and Papilio canadensis Rothschild and Jordan (Lepidoptera: Papilionidae) oviposition preference differences. The 'cold pocket' hypothesis predicted that these sites were climatically distinct, with Vanderbilt the coolest site and Cross Village the warmest; that phenology in the 'cold pocket', Vanderbilt area, would be delayed; and that oviposition preference by 'cold pocket' P. canadensis butterflies would be for white ash.

Every year with regard to total degree-day accumulations, Vanderbilt was the coldest site. Vanderbilt was cooler than the other sites only sixteen times in twenty—nine years during the time period when P. canadensis butterflies were actively selecting host plants (March lst — July 5th). In the years of this study, 1996 and 1997, host plant phenology was not delayed in the 'cold pocket'. In 1996 and 1997, P. canadensis butterfly populations from across Northern Michigan did not show oviposition preference differences. In 1996 and 1997, butterflies from the 'cold pocket' did not show an oviposition preference for white ash. These results indicated a greater depth and complexity to climate/ plant/ herbivore interactions than previously assumed by the 'cold pocket' hypothesis.

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Introduction

Climate, Plant and Herbivore Interactions

"The action of climate seems at first sight to be quite independent of the struggle for existence; but in so far as climate chiefly acts in reducing food, it brings on the most severe struggle between the individuals whether of the same or of distinct species, which subsist on the same kind of food." (Darwin 1859). The interaction between climate, plants and herbivores has been at the center of a great deal of ecological, environmental and evolutionary research. Basic aspects of biology are rooted here; population dynamics; nutrient flow and stabilizing mechanisms in ecology (Hairston et al. 1960); and coevolution of host plants and their herbivores (Thompson 1994) are ecological phenomenon where understanding is advanced by studies of climate, plant, and herbivore interactions.

Examining effects of predation and climate, in addition to phytochernistry, might further clarify plant/ herbivore relationships, as some scholars have suggested that phytochemical coevolution theories do not fully express the depth or variation found in plant/ herbivore relationships (Smiley 1978, Janzen 1988, Bemays and Graham 1988). A recent variant on the topic of plant herbivore relationships and the role of climate is the geographic mosaic theory of coevolution, which posits a coevolutionary relationship continuum in which interactions vary in intensity and expression within a species range (Thompson 1994). This theory incorporates the effects of abiotic variance, such as climate differences, on plant-herbivore interactions. Although much ecological research

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has delved into climate/ plant/ herbivore interactions, understanding is far from complete.

Plausibly, a variety of climatic factors could influence plant herbivore interactions, of which regional warmth or coolness, humidity and precipitation are but two examples (Barbosa 1988). A convenient measure of the former characteristic is thermal-unit accumulation. Host plant phenology has also been implicated in affecting herbivore selection, especially in cases where there are changes in environmental conditions (Barbosa 1988). Constraints on thermal units have been shown for latitudinal clines that can effect host choice (Scriber and Lederhouse 1992). This 'voltinismsuitability' hypothesis has been extended to local 'cold pockets' not simply latitude (Scriber 1996a).

The voltinism-suitability hypothesis has its wide-reaching roots in basic tenets of plant/ herbivore interaction theory. The tenets include factors that drive plant/ herbivore interactions and herbivore range. There are questions as to whether secondary phytochemistry, predators, and the environment are more important to herbivore population control and dynamics. Often, the range of suitable host plants can limit the distribution of associated herbivores. Host plant distribution can be limited by environmental conditions, particularly temperature. This could effect the distribution, development time, and fitness (Cockrell et al. 1994) of the associated herbivores.

Temperature can also affect the number of generations an herbivorous insect can complete in a growing season. Butterflies may make behavioral and physiological adjustments to prevailing weather conditions (Cockrell et al. 1994). In areas where the herbivore may not be able to complete one or two generations, as the area is thermally constrained, there are selection pressures on the herbivore to feed on the plant that will

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most enhance growth. For monarch butterflies, it was shown that latitude and oviposition date can influence the maturation time and the number of generations. Earlier oviposition dates had greater influence on maturation time of larvae than later oviposition dates (Cockrell et al. 1994). In addition to latitude, oviposition date, and climate differences affecting herbivorous insect behavior, growth, distribution and survival, host plant quality is also important. Not all host plants are equal in suitability for larval growth. Growth of many insect larvae is nitrogen limited (Mattson 1980, Scriber 1984a and b, Mattson and Scriber 1987). Since foliar nitrogen content and leaf water are correlated (Scriber and Slansky 1981, Mattson and Scriber 1987), larvae on leaves with low leaf water tend to grow more slowly (Scriber 1977). In areas that are thermally constrained, a herbivore that feeds on a more suitable host plant has an increased chance of pupating before the end of the season. In areas where the number of generations is not thermally constrained, selection pressures are lifted and herbivores are able to feed on a wider number of host plants successfully.

The interaction of thermal units and host plant distribution may create a dynamic interaction in which herbivore/ plant interactions vary across space and time, causing local specialization patterns for a polyphagous species. Evidence has indicated that some species of Papilio have an extremely localized oviposition preference in relation to thermal accumulation or phenology. These butterflies oviposit on leaves that are in full sun, or that may have higher water content (Grossmueller and Lederhouse 1985). In summary, in areas with a short growing season, there is selection pressure for a herbivore to consume a high quality food source that allows it to reach maturity earlier, albeit of smaller size (Ayres and Scriber 1994). The voltinism—suitability hypothesis is the direct

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predecessor to the cold-pocket hypothesis.

Papilio canadensis (Rothschild and Jordan) butterflies, their oviposition host plants and their larval performance have been studied as an example of climate/ plant/ herbivore interactions. These butterflies are excellent research organisms because they are common, showy, strong fliers, and have a variety of interactions with different host plants from extreme specificity to a great deal of polyphagy (Scriber 1995). Oviposition preferences within the *Papilio* group form a particularly intriguing way by which to test interactions, as part of the oviposition preference is genetically based and some of the genes effecting oviposition preference have been localized to a single chromosome (Thompson 1995). Oviposition preferences may be influenced by a variety of factors.

Not all oviposition sites afford similar nutrition, cover, and protection for larvae and adult butterflies. In the landscape of available oviposition sites, some sites are more rewarding. Since larvae generally do not move between sites, ovipositing female butterflies that choose oviposition sites that ensure the greatest fitness for offspring and survival of their genes would be reproductively successful. Because of their catholicism, choice of oviposition sites might be cued by the environmental situation during the flight season. The cues used by the butterflies could include visual ones, such as leaf shape (Rausher 1980, Papaj 1986, Renwick and Chew 1994), tactile ones, such as leaf toughness, and sensory responses to leaf chemical components (Renwick and Chew 1994). Larval growth potential need not be the only important consideration. Larvae may also be susceptible to host-specific predators or parasitoids (Thompson and Pellmyr 1991). In order to reduce the probability of being attacked by predators and parasitoids, some larvae use a form of crypsis (Thompson and Pellmyr 1991), but tree characteristics,

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such as secondary phytochemistry that reduce effects from parasitoids and predators, might be important selection factors (Thompson and Pellmyr 1991).

The direct measure of larval fitness and hence reproductive success of a test species follows the rearing of larvae to adults in the natural environment and determination of survival to sexual maturity. Survival in the field would also provide an estimate of natural levels of mortality. Indirect measures, more amenable to controlled experimentation, include pupal weight, length of time until pupation, and survival of the larvae. If oviposition preferences were being driven by qualities intrinsic to the host plant there could be a correlation between larval performance and host plant quality. If the system is being driven by extrinsic factors, those that increase the survival for the butterfly, but not necessarily for the larvae (Thompson 1988, Thompson and Pellmyr 1991), there should be less correlation between larval performance and oviposition preference for a host plant.

'Cold Pocket' Hypothesis:

In the Northern Lower Peninsula of Michigan, and in the Western Upper Peninsula of Michigan, there are areas of lower average annual frost-free days compared to nearby areas, known as 'cold pockets' (sensu Scriber 1996a). In these areas with a constrained growing season, it is implied that plant phenology and bud-break are delayed (Johnson and Scriber 1994, Scriber 1996a). It was observed that in these 'cold pocket' areas, P. canadensis butterflies preferred Fraxinus americana L., white ash, as an oviposition host plant (Johnson and Scriber 1994). Studies outside 'cold-pockets' had

shown white ash to be of poor quality for hosting larval growth (Johnson and Scriber 1994) because ash quickly declines in some forms of soluble nitrogen and increases in leaf toughness after bud-break (Hunter and Lechowicz 1992). The 'cold pocket' hypothesis posits that white ash would not be as poor a host inside as it was outside of the 'cold pocket' as white ash, a late bud-breaking plant, would be even further delayed in bud-break in the 'cold pocket' (Scriber 1996a). White ash would be younger, with higher water content at the time that P. canadensis is flying. P. canadensis, if selecting leaves that increase larval performance, would choose these delayed white ash leaves as they would be more nutritive, with higher water content, an increase in some forms of soluble nitrogen, and with a lower leaf toughness. The increase in larval performance relative to other host species would not be seen on white ash outside the 'cold pocket' (Scriber 1996a).

Other rationales to explain the localized P. canadensis white ash oviposition preference have been proposed. These include the possibility that P. canadensis competes for resources with major forest defoliators such as Malacosoma disstria (Hübner), forest tent caterpillar, and Lymantria dispar L., gypsy moth (Scriber 1996a; Scriber and Gage 1995). As gypsy moth is known to avoid white ash as a host plant P. canadensis might be driven to utilize white ash in the face of such competition (Scriber 1996a). However, gypsy moth is a recent arrival to Michigan (Scriber and Gage 1995) and it seems unlikely that in 6-8 years gypsy moth would have driven P. canadensis to a white ash preference. P. canadensis preference for white ash has been observed in competitor—free laboratory trials (Scriber 1996a, Johnson and Scriber 1994), also suggesting that the choice was not due solely to forest pest outbreaks. Additionally, these

forest pests do not occur in all of the 'cold-pockets', such as in the Upper Peninsula of Michigan, in which the oviposition preference shift was observed. Lastly, these two pests do occur in conjunction with P. canadensis outside of 'cold pocket' areas and where white ash is not a preferred host.

Papilio canadensis:

Papilio canadensis is a species in the Papilio glaucus L. group, and as a species only recently has been separated from P. glaucus (Hagen et al. 1991). The range of P. canadensis corresponds to the Pleistocene glaciation area of Northern America and constitutes a significantly distinct ecotone (Scriber and Gage 1995), extending from the Appalachian mountain range into the Great Lakes area, and north across Canada and Alaska (Hagen et al. 1991). The adaptations of P. canadensis for life in cold climates (Kukal et al. 1991, Ayres and Scriber 1994) as well as their ability to detoxify a great variety of plant allelochemicals, such as tremulacin from quaking aspen and other Salicacious plants, and prunasin from black cherry, demonstrates the successful escape from its tropical ancestry of the Papilionidae (Scriber 1995).

P. canadensis is a univoltine butterfly (Hagen and Lederhouse 1985), spending four to eight months of the year as a pupa, often buried under snow. In order to avoid eclosing before the temperature is sufficient to maintain metabolic and dietary needs, P. canadensis must be tuned in to local climate factors, such as precipitation and day length. Once it has emerged, it spends its three to six week adult life span (Scriber 1996b) feeding, mating and ovipositing. P. canadensis emerges from its puparium in late May

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(Scriber 1996b). P. canadensis is protandrous in most years, with males emerging slightly before females (Lederhouse et a1. 1995). Early emergence allows males greater access to females (Ae 1995), as well as salts and minerals (Lederhouse et a1. 1990) that are possibly used for spermataphore construction (Lederhouse et al. 1990). A mature male patrols from site to site seeking receptive females (Brower 1959), chases, courts and attempts to copulate with a receptive female. Papilio butterflies are polygamous, with females sometimes mating five to six times (Scriber 1996b). After a mating, the female stores the spermataphore of the male in her bursa copulatrix, and may utilize the sperm of the most recent mating to fertilize her eggs (Scriber 1996b). After transfer of the spermataphore, females search for oviposition sites.

Upon alighting on a host plant, a female swallowtail uses her forelegs in a drumming behavior to ascertain host plant quality (Nishida 1995). She approaches the leaves, and curling the tip of her abdomen forward (Nishida 1995), deposits a single egg on the plant surface (Scriber 1996b). Eggs when freshly laid are a deep green, blending into the leaf surface color. As the embryo within the egg matures, the egg becomes deeper in color, and is almost brown at the time of ecdysis. After ecdysis, the larva eats the chorion of the egg in order to obtain some early nutrition, or perhaps to remove evidence of its presence from potential natural enemies (Scriber 1996b). The larva feeds on the leaves of the plant on which it was oviposited. If the plant has toxic chemicals, is low in nutrition, subject to desiccation, signals predators to feed on the larva, or affords little protection, the larva is less likely to survive.

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P. canadensis is a polyphagous butterfly, unusual in the butterfly world because of the high degree of polyphagy, with adults and larvae utilizing a variety of host plants for feeding and oviposition (Scriber 1984a). P. canadensis can utilize plants from the families Salicaceae, Oleaceae, Rosaceae, Tiliaceae, Lauraceae, and others (Scriber 1984a). As P. canadensis host plants are trees, they are usually apparent and enduring, ensuring that P. canadensis can actively seek and oviposit on a host plant rather than lay eggs haphazardly (Wiklund 1984).

The trees investigated for oviposition preference by P . canadensis are listed in Table 1. For each, the northern portion of Michigan is roughly in the middle of its range. There are differences among the trees in preference for soil type, tolerance for shade, tolerance for water stress and other characteristics, as might be expected (Voss 1985, 1996, Crow 1990, Marquis 1990, Safford et al. 1990, Schlesinger 1990, Perala 1990). Of particular importance for this project is that bud-break depends on thermal accumulation with quaking aspen (Michaux) (Perala 1990) and paper birch (Marshall) (Safford et al. 1990) breaking bud early; and basswood (L.) (Crow 1990) and white ash (L.) (Schlesinger 1990) breaking bud late. Black cherry (Ehrhart) breaks bud intermediately (Marquis 1990).

The present study investigated P. canadensis oviposition preference in relation to larval performance using host material from areas with decreased thermal accumulation and from areas of greater thermal accumulations. Climatic differences at three different locations in Northern Michigan were characterized. Water content of host leaves in 1996 and 1997 was measured. Oviposition preference and larval performance experiments were carried out with a variety of P. *canadensis* populations in Northern Michigan in

1996 and 1997. The 1996 growing season was climatically typical for the region, while 1997, an El Niño year, was dryer and colder across the state. A few updating observations were made in May and June of 1998; both months were hot and dry.

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Sites:

The surveyed sites covered a range of growing seasons based on the average number of freeze-free days as described by the Michigan Climatic Atlas (Eichenlaub et a1. 1990, Scriber 1996a). The first site was the Pellston area (Pellston Plains; on Catsmanfls comer; to the intersection of Riggsville Rd. and Bryant Rd., Emmet and Cheboygan counties). Pellston averages 90-100 freeze-free days in the growing season. The Vanderbilt area, a 'cold pocket', (near Vanderbilt in Pigeon River State Forest, on the border of Cheboygan and Otsego counties) was the second site. Vanderbilt averages 70 freeze-free days in the growing season. Thumb Lake was 'added' to the Vanderbilt site only for occasional collection of 'cold pocket' butterflies. For some oviposition preference trials, yields of Vanderbilt test organisms were inadequate for the experimental protocol and Thumb Lake specimens were taken to supplement Vanderbilt ones (Thumb Lake averages around 90 freeze-free days in the growing season). A third area beside Lake Michigan, near Cross Village, Wycamp, Hardwood State Forest (Emmet county) was examined. Cross Village averages 140-150 freeze-free days in the growing season. No butterflies collected from Cross Village laid any eggs. Most of the butterflies collected from Cross Village were collected early in the flight season and may have been unmated. In order to compare oviposition preferences of an outlying population of butterflies, butterflies were collected from across the Upper Peninsula and employed. The Upper Peninsula (Chippewa County) averages 110-130 freeze-free days; (Iron County) averages 70-90 freeze-free days; (Dickinson County) averages 100-110 freeze-free days.

Methods:

Climatology:

Daily degree-days were calculated using the averages method (Pedigo and Zeiss 1996) with a general insect threshold temperature of 10°C. Climate data from the three sites, from 1969-1997, were obtained from the Department of Geology, Climatology Lab, Michigan State University. These years had almost complete data sets across the sites. Three time periods were examined. The first time period was the seasonal accumulated degree-days (March lst - October 3 lst). The 'cold pocket' hypothesis assumed climate differences across Northern Michigan based on seasonal freeze-free day differences, roughly correlated to seasonal accumulated degree-day differences. In order to make comparisons within the framework of the 'cold pocket' hypothesis, it was necessary to examine climate differences at this level. Degree-day accumulations that occur after leaf senescence and after larvae pupate, may contribute to overall degree-day accumulations, but are not very interesting biologically. Early season degree-day accumulations however, may be very important to the biological systems studied here. Early season degree-day accumulations can influence bud-break, leaf flush, and butterfly eclosion. For the next two analyses of degree-day accumulations, late season degree-day accumulations were excluded, and early season degree-days were included. Another time period examined was the flight and larval development season accumulated degree days (March lst - July 3 lst). This time period included early season degree-day accumulations, the degree-days accumulated during the P. canadensis flight season (usually confined to June, sometimes occurring earlier in May), and during the time period when larvae were

developing. The third time period examined was the flight season accumulated degreedays, (March lst - July 5th). This time period included early season degree-day accumulations, and the degree-days accumulated during the P. canadensis flight season.

Degree-days (threshold temperature 10°C) accumulated in Vanderbilt for May, June, July, and August for each year, 1987-1997, were divided by the amount of precipitation in Vanderbilt in millimeters. Vanderbilt was the only site that had both reliable precipitation and thermal unit data. Such heat/ precipitation indices are good for indicating drought stress conditions (Gage, 1998).

Phenology:

Leaves were collected in 1996 from Pellston and Vanderbilt. Leaves were selected without conscious bias from several trees of each of five species: black cherry, paper birch, white ash, basswood and quaking aspen. Collections were made on nine dates between June 3 and July 23, although not all hosts were sampled from both sites on each date. There were at least four collection dates per species per site. Leaves were immediately placed into plastic, airtight bags and stored on ice. They were categorized by site, date and species. For water content determination, leaves were weighed the same day as they were collected, placed into a drying oven set at 50°C, for 3-4 days. Dry and wet weights were used to calculate percent water content.

In 1997, leaves were collected from all three sites. There were 38 collection dates between May 23 and August 13. Due to the labor-intensive nature of the sampling regime, Vanderbilt leaves were usually collected a day later than Pellston and Cross

Village leaves. Ten leaves of each species per date, per site, were processed.

Relationships among leaf water weight, tree species, site of origin, and date were examined using a stepwise regression analysis, with yearly data analyzed separately, then combined, to determine if there were year to year differences in phenology.

Oviposition Preference:

Four oviposition assays were carried out. In each, there was one butterfly, and one leaflet, leaf, or set of leaves per treatment per chamber. Lifetime assays were run (until the butterfly was weak or exhausted). Forewing length measurements and age estimates, as described by Lederhouse and Scriber (1987), were made on field-collected females before each was assigned a brood number and distributed to an oviposition preference trial. Leaves, of approximately equal surface area, refrigerated less than seven days were used. The leaf petiole was placed into a water-filled plastic aquapic. Random placement of all host plants in each array, around a clear plastic multi-choice oviposition chamber (25 cm diameter by 9 cm height) ensured that oviposition results were uninfluenced by sequence. Oviposition dishes were stacked on a rotating turntable (6 turns/h) lit by 60-watt incandescent bulbs (6h light-dark cycles) (Scriber 1993). Temperature inside the oviposition dishes was maintained near 30°C during peak oviposition times, when the oviposition dishes were illuminated to simulate daylight. Butterflies were removed from oviposition dishes and fed a 20% honey solution daily while eggs were collected and counted. Eggs on the paper liner, or plastic chamber were counted as on ^a leaf if they were within ¹ cm of the leaf. If the egg was more than ¹ cm

from the leaf, they were counted as laid on a plastic or paper surface, which was considered a 'leaf type' in analysis. Leaves with eggs present were removed and stored (27°C) for larval assays. Positions were refilled with fresh foliage of the same species. The replacement foliage was not necessarily from the same tree or collection date. In all cases, the foliage was from the same site.

Five choice array: Adult female P. canadensis were presented simultaneously with leaves of white ash, basswood, paper birch, black cherry and quaking aspen collected either in Pellston (1996 and 1997) or Vanderbilt (1997). Butterflies were collected from the Vanderbilt area (17 in 1996, 19 in 1997) and from outside the Vanderbilt area (54 in 1996, 16 in 1997).

Young and old white ash array: In 1998, an oviposition array consisting of two types of white ash foliage was tested. The two types were older, fully expanded leaves (collected from Okemos, Michigan) and young unexpanded leaves (collected from near the 'Mystery Spot' in Chippewa county). Butterflies were collected from Vanderbilt (n=2) and five other sites across Northern Michigan and the Upper Peninsula (n=13.)

Phenology array: In 1997, oviposition arrays consisting of white ash foliage collected from the three principal sites, plus one more, were tested. The fourth site, in Okemos, near Michigan State University, was outside the geographic region, and south of the range of P. canadensis. Butterflies were collected in Vanderbilt (n=6) and outside this area $(n=6)$.

Chemical extract array: White ash leaflet material was collected from four sites: Pellston, Vanderbilt, Cross Village and Okemos. Leaves from Pellston were collected on 10 June 1997 and 24 June 1997; and extracted on 16 June 1997 and 27 June 1997. Vanderbilt leaves were collected on 4 June 1997 and 11 June 1997; and extracted on 5 June 1997 and 16 June 1997. Cross Village leaves were collected on 10 June 1997 and 24 June 1997; and extracted on 16 June 1997 and 30 June 1997. Okemos leaves were collected on 12 June 1997 and 24 June 1997; and extracted on 16 June 1997 and 26 June 1997. The leaflet material (petiole and rachis not included) from each site, on each extraction date was placed in a sterile liquid nitrogen cooled mortar and pestle and roughly ground. This material was then placed in a sterile Electric Coffee and Spice Grinder (Regal, Kewaskum, WD and ground until the material was homogeneous, and fine. Thirty to forty g's of the dispersion was placed in ^a filtration column (149 mm ^x 450 mm) that had been packed with cotton swabbing, and methanol (175 mL) was added. (An oviposition assay in 1996, testing Papilio glaucus oviposition preference for white ash extracts found a higher response to methanol rather than hexane or ethyl acetate. Extracts in 1996 were also solubalized in acetone and sprayed onto quaking aspen leaves with a plant sprayer.) After 30 min., the column stopcock was opened and effluent was

collected. The stopcock was closed, and the collected effluent was added back to the column. This process was repeated two times. After the effluent was collected a third time, the solubalized extract was concentrated in a rotovap (Brinkmann Instruments Inc., Westbury, NY) at 100 °C (there was not a successful vacuum created by the rotovap setup used), until all volatile components had been removed. The residue was weighed and acetone was added to make a $1g/1L$, or 10% suspension. Using a plant sprayer, this was sprayed to saturation onto quaking aspen leaves that were placed in oviposition arenas. Ovipositional responses to such extracts, from Pellston, Cross Village, Vanderbilt and Okemos, were measured and compared to the response to leaves sprayed with acetone alone and water alone. Butterflies were collected from Vanderbilt (n=4) and from outside Vanderbilt (n=5).

Larval growth:

Eggs were placed in dishes marked with a brood number and the host plant preference of the mother. Mother preference was defined as the oviposition host plant with the highest percentage of eggs. Dishes were stored in a Percival growth chamber at 27 °C (18 L: 6 D) and checked daily for eclosion. When neonates emerged, all larvae from the same brood were distributed randomly to a feeding assay on black cherry, paper birch, white ash, quaking aspen or basswood leaves. Few larvae were set up on paper birch or basswood in 1997, as these were found to be poor hosts in 1996. No more than five or six larvae per dish were assigned to initial feeding assays. Larvae were reared at 27 °C (18 L: 6D) in Percival growth chambers. Larvae were checked every two to three

days (or more frequently if leaf material was rapidly consumed), the dishes were cleaned, leaf material replaced, and the date, number of surviving larvae, and the instar of each larvae were recorded. When the larvae reached the third instar they were separated and reared in individual dishes to reduce crowding effects. After pupation, they were weighed to the nearest 0.0001g and sexed. Weight, length of time to pupation, length of time in each stage of metamorphosis and overall survival were recorded. Overall survival was the percentage of neonate larvae that pupated relative to the number set up on the host plant.

Statistical analyses:

Data were analyzed in spreadsheet format using Microsoft Excel 5.0 (Microsoft, 1994). Normality was confirmed with the Shapiro-Wilkes tests in the proc univariate program (SAS Institute Inc., 1989). Climate data were analyzed with proc glm in SAS to observe statistical differences in mean degree-day accumulations between sites; and using proc reg in SAS to investigate relationships between year, site and accumulated degreedays. As Cross Village data were not complete for the 1985-1997 period, missing years were excluded from regression and analyses of variance. Phenology data were analyzed using proc reg in SAS for 1996, 1997 and the two years combined to probe relationships between site, date, accumulated degree-days, host-plant species, year, and foliar percent water content. Oviposition data ratios were arcsine transformed and analyzed using proc glm in SAS with an ANCOVA where approximate butterfly age and winglength were covariates. Statistical significance was assigned at α = 0.05 using Fishers least significant

difference test.

The most important contributing factor to significant interactions was determined by slicing the interactions in SAS. All reported means and standard errors are least square means as these means and standard errors are adjusted as if the design had been balanced. They provide a population marginal mean, and allow that the sum of oviposition preference ratios will add to one. Mean pupal weight differences were analyzed using proc glm in SAS with an ANOVA to uncover significant differences in pupal weight attributable to pupal sex or host-plant. Mean days to pupation differences were analyzed using proc glm in SAS with an ANOVA to discover significant differences in the days to pupation attributable to pupal sex or host-plant. Difference in survival of larvae per instar (where the larval host plant, the mother's oviposition preference, the instar the larva was in, and the length of time the larva spent in that instar were variables) was analyzed with a repeated measures analysis in proc mixed in SAS, with the covariance parameter estimate as a diagonal arcsine model.

As there is some concern as to how a butterfly's oviposition preference should be weighted, the oviposition assays were examined using an additional protocol. In this analysis, only butterflies that laid a minimum of ten or more eggs were included. The cut-off value of ten was used, because this was the historical cut-off value in prior examinations of the 'cold pocket' hypothesis. While this analysis may skew the results in favor of butterflies that lay more eggs, it minimizes the chance that the results may be skewed by butterflies that lay few eggs, and may not really exhibit host plant preferences. This statistical analysis was conducted in the same manner as the above, with the

exception that butterflies laying fewer eggs were excluded.

Results:

Climatology:

Over the time for which comparable data were available (i.e. 1969-1986), generally, Cross Village had the largest average number of accumulated degree-days and Vanderbilt the smallest. This was true whether or not one was examining accumulated degree-days for the season (March 1st - October 31st); early season to the time of pupation (March lst - July 3 lst); or the early season and the butterfly flight period (March lst - July 5th) (Table 2).

Mean seasonal accumulated degree-days, March 1st – October 31st, were significantly different between Vanderbilt and the other two sites (p<0.0001); and Pellston and Cross Village (p < 0.05). Mean flight and larval development accumulated degree-days, March 1st – July 31st, were significantly different between Pellston and Cross Village (p <0.002) and Vanderbilt and Cross Village (p <0.0001). There was no statistically significant difference for this period between Pellston and Vanderbilt. Mean flight season accumulated degree-days, March 1st $-$ July 5th, were not statistically significantly different between Vanderbilt and Cross Village; Vanderbilt and Pellston; and Pellston and Cross Village. In 5 years of 29 the difference in seasonal degree-days between Vanderbilt and Pellston exceeded 200 at July 3 lst. In 5 years of 29 the difference between Vanderbilt and Pellston at July 5th exceeded 100 (Figure 1).

Vanderbilt showed a significant warming trend in total seasonal accumulated degree-days (Figure 1). For the two shorter periods, trends in the Vanderbilt accumulated

degree-days, while positive, were not statistically significant. Neither Cross Village nor Pellston showed any persistent trends over 29 years.

For all three time intervals, the year to year variance in accumulated degree-days was greater than site to site variation in accumulated degree-days. Stepwise analysis for the flight season degree-day accumulations, March lst - July 5th, removed site differences from the model, as it didn't add to the power of the regression, showing that site differences were not significant (Table 3).

As precipitation differences and water stress could influence host plant quality for larval growth, heat/ precipitation indices are of particular relevance to this project. Heat/ precipitation indices (Figure 2) for the Vanderbilt area for years 1987-1997 indicated that May, 1997, was the driest of all Mays and that 1997 had the second most drought-like June. (June 1991, had a higher heat/ precipitation index and was both hot and dry.) July and August of 1997 had heat/ precipitation indices similar to those of other years.

Phenology:

In 1996, leaf water content varied among tree species, i.e. interspecifically, and collection date, i.e. seasonally (Table 4). However, within a given plant species, and on a particular date there were no site differences (Table 4). When data were adjusted for degree-day accumulations, stepwise regression analysis kept all factors in the regression model, but site differences were the least important (Table 4). Water content declined in tree leaves throughout the season, with quaking aspen and paper birch having high water content early in the season, with water contents declining earlier, and basswood and white

ash maintaining a high water content longer (Figure 3).

A greater number of phenological assessments were made in 1997, using three sites, five host plant species, and nineteen dates. Leaves were indexed early, before budbreak of some species, so that bud-break and early leaf flush water contents could be recorded for some species, providing a clearer picture of water content and suitability for larval nutrition. Stepwise regression analysis on these data showed that leaf water content varied with tree species (interspecifically), collection date (seasonally), and with site (Table 5). The contrast with 1996 results was explored by stepwise regression on leaf water contents at the sites (Pellston and Vanderbilt) common to both years. Similar regression results were found, both with and without adjustment for degree-day contributions when Pellston and Vanderbilt were compared, and when Pellston, Vanderbilt and Cross Village were compared. Site contributions were the least meaningful contributor to the regressions (Table 6). As in the previous set of measurements, leaf water content declined throughout the 1997 season for all species. Across all three sites, quaking aspen and paper birch had high water content early in the season and water content declined rapidly early; basswood and white ash did not break bud as soon, but maintained a high water content later (Figure 4).

Data for Pellston and Vanderbilt for the years 1996 and 1997 were compared (Table 7). Stepwise regression indicated that leaf water content varied seasonally, interspecifically, geographically, and annually. When these data were degree-day adjusted, annual variation remained a significant factor, second in importance to seasonal influence (Table 7).
Oviposition Preference:

Five choice array: In 1996, oviposition preference was attributable to species of host, but not butterfly origin (Table 8). P. canadensis preferred to oviposit on quaking aspen, with 29.8% of eggs laid on these leaves when the data was pooled (Figure 5). Significantly more eggs were laid on quaking aspen by the P. canadensis test group than on any other leaves. For pooled data, quaking aspen and white ash did not have a significantly different number of eggs laid on them. Black cherry and basswood did not have a significantly different number of eggs laid on them. Paper birch and the chamber paper were also not significantly different from each other in the percentage of eggs laid on these substrates. All three groups were significantly different from the other two groups (Table 8). Using a cut-off value of ten eggs per female for inclusion in the analysis did not change the results, or effect the significance of any of the factors.

In 1997, neither the origin of the butterfly, nor the site of origin of the leaf material was correlated to host preference (Table 9). Again there was an oviposition preference attributable to tree species. Oviposition preference was greatest for black cherry, with 29% of the total eggs laid on these leaves when data were pooled for leaves from the Pellston (Figure 6) and Vanderbilt (Figure 7) sites and for butterfly location. Mean percent eggs laid on a treatment were similar for: white ash, basswood and quaking aspen; basswood, quaking aspen, paper birch and chamber paper; black cherry was significantly different from all other treatments (Table 9).

Using a cut-off value of ten eggs for inclusion in the analysis did slightly change the results. In this case, the origin of the host plant, and the origin of the butterfly did not significantly affect the oviposition preference. However, the species of tree, the interaction of the butterfly origin and the species of tree, and the interaction of the origin of the host plant and the species of tree were all found to be significant. When the butterfly origin by species of tree interaction was examined, it was found that tree species contributed most significantly to oviposition preference except for butterflies from Vanderbilt; the butterfly origin contributed significantly to the interaction on black cherry host plants. When the tree collection site and tree species interaction was compared, it was determined that the tree species contributed most significantly to the interaction. Mean percent eggs, with a cut-off value of ten, laid on a treatment were similar for: black cherry, white ash, and quaking aspen; basswood and quaking aspen; basswood and paper birch; and paper birch and chamber paper.

Young and old white ash array: There was no difference in preference attributable to butterfly collection site. There was a significant difference in preference for young, unexpanded white ash leaves, versus fully expanded white ash leaves, versus a paper (no leaf) control. When data were pooled, the most eggs (Table 10, Figure 8) were laid on the unexpanded white ash, and the least eggs laid on chamber paper (Table 10, Figure 8). An intermediate number were laid on the expanded older white ash leaves (Table 10, Figure 8). The interaction of butterfly collection site and white ash phenology was also significant. When this interaction was examined, it was determined that the white ash age contributed most strongly to every interaction, except that white ash age did not affect

oviposition preference for butterflies collected from Charlevoix or butterflies collected from Vanderbilt. Both of these populations consisted of two or fewer butterflies. It was also determined that the butterfly collection site did significantly affect oviposition preference for old white ash leaves. When the data was examined with a cut-off value of ten eggs, there was no difference in the results.

Phenology array: There was no significant difference in preference for different phenological stages of white ash as indexed by four collection sites by all butterflies tested (Table 11). Differences in preference by butterflies from the Vanderbilt area versus the Pellston area were not significant (Figure 9). The sole significant difference between treatments was that fewer eggs were laid on chamber paper than on any of the foliage treatments (Table 11). When analyses were performed with a cut-off value of ten eggs, there were no differences in the results.

Chemical array: There was no preference difference by all butterflies tested for methanol extracts of white ash collected from four different sites or the controls (Table 12, Figure 10). When analyses were performed with a cut-off value of ten eggs, there were no differences in the results.

Larval Performance:

Overall survival from neonate to pupa in 1997 was low. No larvae reared on paper birch and basswood survived to pupation. The survival of larvae on black cherry was 33%, followed by quaking aspen, 13.5%, then followed by white ash, 7.3% (Table 15, Figure 11).

Survival in each instar in 1997, with host plant, host plant preference by the ovipositing female, larval instar, and days per instar showed that the host plant and the days per instar were important and significantly different in percent larval survival in each instar (Table 13).

Pupal weight varied depending upon the host plant species in 1996. Pupal weights on black cherry, quaking aspen, and white ash were not Significantly different, although the least square means were higher on quaking aspen, followed by black cherry, followed by white ash (Table 14). Pupal weight on basswood was similar to weight on white ash (Table 14, Figure 12).

In 1997, there was a (1: 1) ratio of pupal males to females (72 males: 78 females). Variation in pupal weight was examined by looking at differences explained by the rearing host plant, and the sex of the individual. The pupal weight was mainly explained by host plant (Table 15). Pupal sex, and the sex by host plant interaction were not significant contributors to pupal weight. Pupal weights were highest for larvae reared on

black cherry, and were significantly different than the weights of larvae reared on white ash and quaking aspen (Table 15, Figure 13).

Days to pupation: Time to reach pupation was also examined as a fitness indicator. In 1997, the length of time it took to reach pupation was not statistically dependent on host plant, pupal sex, or the sex by host plant interaction. Although duration to pupation was not explained by host plant, individuals on quaking aspen seemed to reach pupation slightly faster than other individuals, and the males even faster than the females, but this trend was not significant (Table 16, Figure 14).

Discussion:

Papilio canadensis, the Canadian tiger swallowtail, is common throughout the Northern United States. Adults emerge in early summer, nectar, mate and females lay eggs on a variety of plants. The eggs ecdyse and the neonates feed, develop and pupate all within a few weeks (Scriber 1996b). The larvae usually stay on the same leaf, at least in the first two instars and thus selection of oviposition sites by the egg-laying female is important (Watanabe 1995). If she selects ^a site less suitable for the growth, development and survival of offspring, her fitness, in an evolutionary sense, is inferior. Oviposition preferences may be driven by intrinsic factors such as chemical cues of the host plant that reflect nutritional quality or that are feeding deterrent toxins, and by extrinsic factors such as protection from predation (Thompson 1988, Thompson and Pellmyr 1991). Many studies implicate allelochemicals in the process (Feeny 1995).

Some areas of the Northern Lower Peninsula of Michigan have fewer degree-days of thermal accumulation and fewer frost-free days over the growing season than other areas. It is proposed that P. canadensis has an oviposition preference for white ash as a host plant in colder areas, in contrast to warmer areas, as delayed white ash bud-break and leaf development would be better suited relative to other hosts to nurture rapid larval growth (Scriber 1996a). This 'cold pocket hypothesis' was a local modification of the voltinism-suitability hypothesis (Scriber and Lederhouse 1992). The purpose of the present project was to search for an effect of climate on oviposition preference of P. canadensis. It was supposed that host plants, which depend on accumulated degree-days in seasonal development, would be of different attractiveness in warmer and colder areas

during the P. canadensis flight period, and that egg-laying females would differentially select among hosts in such areas.

White ash was predicted to be the preferred host plant for oviposition in the 'cold pocket', and larvae were predicted to perform better on white ash. Oviposition preference did vary with inter-specific differences in host plant, and with large differences in host plant phenology (newly flushed vs. older, tougher foliage). As host plants may vary in suitability for larval growth, inter-specific differences in host-plant quality are well documented and not surprising. Newly flushed leaves tend to have a higher percent water content and decreased concentration of certain 'quantitative' defensive compounds (Feeny 1976). As water can be a limiting factor for larval growth and defensive compounds can reduce or slow larval growth, that butterflies would prefer to oviposit on newly flushed leaves is also not surprising. There is some evidence in the literature that indicates that leaf age and bud burst phenology can play a role in oviposition preference (Hunter 1992, Hunter et al. 1997, Scriber and Slansky 1981). In a study with winter moths, Hunter et al. (1997) determined that local population variation was seemingly related to plant quality and budburst phenology. Other studies have indicated that oviposition preference is influenced more by the over-riding importance of inter-specific plant differences than intra-specific differences in plant quality (Schultz 1988).

Larval performance on the five host plants was examined. Significant differences in pupal weight on host plants were compared to differences in oviposition preference. In 1996, oviposition preference was the same for quaking aspen and white ash; black cherry and basswood; paper birch and chamber paper. In 1996, larval performance was similar on quaking aspen, white ash and black cherry; white ash and basswood. No larvae

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survived on paper birch. Similar differences existed in oviposition preferences and larval performance. In 1997, oviposition preference was not different on: quaking aspen, white ash and basswood; or quaking aspen, basswood, paper birch and chamber paper. Preference for black cherry was greater than in all other treatments. In 1997, larval performance was the same on quaking aspen and white ash. No larvae survived on paper birch or basswood. Performance on black cherry was higher than on all other treatments. Again oviposition preference and larval performance hierarchies were similar. Both oviposition preference and larval performance hierarchies on host plants changed between 1996 and 1997. This change occurred in all populations, and may have been attributable to the dry May and June of 1997.

Neither oviposition preference nor larval performance followed the 'cold pocket' hypothesis predictions in either 1996 or 1997. ^I tested the assumptions of the 'cold pocket' hypothesis, to determine if the initial conditions had been met, and to obtain a better picture of what was occurring in the 'cold pocket' in 1996 and 1997. These assumptions included determining if bud-break and host plant phenology were delayed in the 'cold pocket' and if the 'cold pocket' was a thermally unique area.

In 1996 and 1997, foliar percent water content for five test plants was measured as an index of plant nutritional quality. Foliar water content varied by host plant, time of season and year, but variance due to site was minimal. These data are in agreement with the climate data in that neither data set found site to site variation, but both detected yearly variation. These phenological data support the contention that partial (that is, early) season measurements of climate and foliar water content are important in this biological system as values are high and then taper off.

Twenty-nine years of weather data were available for three areas in the Northern Lower Peninsula. Vanderbilt was always cooler than Pellston and Cross Village when summing total seasonal degree-days (March lst - October 3 lst) and flight and larval development seasonal degree-days (March lst - July 3 lst). The differences in degree-day accumulations between sites were statistically significant for these two time periods. The whole-season difference justified calling the Vanderbilt area a 'coldpocket'. However, accumulated degree-days through the flight season up to July 5th alone, Vanderbilt was the coolest site only (16 times in 29 years), and site differences over this period were not significant. Early degree-day accumulation is most important to the biological processes I examined and differences over flight season among sites were obscured by the magnitude of year-to-year differences within a site. To the extent that climate indirectly influences oviposition preference, one might expect P . canadensis to show as much, or even more, lability in host plant choice across years at a given site, than across sites for a given year. It is also unclear how many catastrophic 'cold' years out of 29 years are enough to exert significant selection on host choice of P. canadensis. When climate data was examined across Northern Michigan, it was determined that the Vanderbilt area was not cooler when compared to nearby areas at a biologically significant time, (March lst — July 5th). Also, when host plant bud-break and phenology were assessed, it was determined that they were not delayed in the Vanderbilt area in 1996 and 1997. The lack of thermal unit accumulation differences, and similar water content data supported the contention that Vanderbilt was not remarkable as a 'cold pocket' during recent flight seasons. As such, the 'cold pocket' hypothesis would predict no difference in the oviposition hierarchy amongst butterflies from these sites; or among

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butterflies for foliage from these sites. Subsequently, white ash should not be preferred as an oviposition host plant, and larvae should not have increased performance on white ash. My results with P. canadensis, were consistent with these observations.

Heat precipitation indices usefully depict one aspect of climatic variability. I prepared such indices for four months of Vanderbilt data from 1987 to 1997. The final year stood out as being unusually dry in both May and June. Dry conditions lead to water stress on a plant. As plant water content decreases, soluble forms of nitrogen increase (Mattson and Scriber 1987, Scriber 1977, Thomas and Hodkinson 1991). White (see Thomas and Hodkinson 1991) hypothesizes that water—stressed plants suffer increased herbivory; this theory is based on the observation that climatically disturbed areas often have insect outbreaks (see Thomas and Hodkinson 1991). Bultman and Faeth (1987) tested the hypothesis by examining leaf miner populations as an indication of predation pressure under water stress conditions (drought achieved by cutting off roots), where water had been added (irrigation) and in control conditions. Their findings contradicted the supposition: Cameraria Sp. B, predicted to decrease, increased in the irrigated treatment; and *Cameraria* sp. A, predicted to increase, decreased in water stress conditions. Other studies also have shown that insect larvae perform less well on plants with low leaf water levels. Larvae on leaves with low leaf water grow more slowly and are less efficient at utilizing nitrogen, and water content of leaves may limit larval growth (Scriber 1977). Water stressed conditions can have consequential impacts on plants and their herbivore communities. The oviposition differences that we saw in 1996 and 1997 may, in some part, be due to the dramatic differences in May and June precipitation between the two years. The aspen seemed especially sensitive.

In summary, thermal unit differences from March lst - July 5th in Northern Michigan differ between years rather than between sites. Plant quality and phenology differences vary by species, by seasonal fluctuations and by year-to-year fluctuations. In comparison, climatic and phenological spatial variations for the three test sites were not remarkable during the period of biological significance for the present project. Vanderbilt was not meaningfully a 'cold pocket' in the 1969-1997 interval at an appropriate time period, and the 'cold pocket' hypothesis could not apply here. Generalist oviposition preferences were labile and showed year to year flexibility. For Papilio canadensis, oviposition preference and larval performance hierarchies were similar. The 'cold pocket' hypothesis will have to be evaluated by comparing areas that differ more in climate during the early part of the year than did Vanderbilt, Pellston and Cross Village over the recent twenty-nine years. Although the whole season (March lst — pupation) selects against oviposition mistakes on the wrong host plant, it is early season differences in host plant quality that the female must evaluate.

Vanderbilt had the lowest seasonal (March lst - October 3 lst) accumulated degree-days over a 29 year period, as compared to Pellston and Cross Village. The flight season (March lst - July 5th) accumulated degree-days did not differ between Vanderbilt, Pellston and Cross Village. Vanderbilt was generally the coldest site (March lst - July 5th), (21 times in 29 years); (March lst - July 3 lst), (23 times in 29 years); (March 1st - October 31st), (29 times in 29 years). Year to year fluctuations in accumulated degree-days were greater than site to site variation. Although there were year to year variations, the Vanderbilt site showed that there was a trend to the variance. This may be indicative of long term climate trends with short-term variation. Hypotheses

based on supposed climate averages for a site may not usefully predict the outcome in any but the most average of years.

The assumptions of the 'cold pocket' hypothesis did not hold true in 1996 or 1997. The 'cold pocket', during the behaviorally critical time period (March lst - July 5th), did not exist. There were no differences in intra specific host plant differences in phenology between the sites. Even considering the limited availability of butterflies, the white ash preference did not exist in 1996 or 1997 (only 19% and 18% in a five choice study respectively). There were no differences in oviposition preference of butterflies from different p0pulations. Larval performance and oviposition preference hierarchies were similar in 1996 and 1997. Larvae did not perform well on white ash in either 1996 or 1997. This leads to interesting speculation regarding the interactions of plants, herbivores, the prevailing climate conditions, and the evolutionary significance of these interactions. The 'geographic mosaic' theory of coevolution describes the evolutionary landscape as dynamic, where coevolutionary relationships are not static across a host species range, but rather are labile in response to host plant distribution, competition and environmental differences, among other factors (Thompson 1994).

Given the nature of the relationships discovered and tested in this project, P. canadensis oviposition preference in the 'cold pocket' readily conforms to the defining principles of the geographic mosaic theory of coevolution. Under a given set of conditions, reduced number of accumulated degree-days and delayed bud-break, generalist herbivore oviposition preference was for a normally poor quality host plant, white ash. When these conditions varied, host plant preference varied. Snapshots of three different climatic conditions resulted in three different oviposition preferences. In

cold years (1992-1995), white ash was preferred. In a thermally average year (1996), with average precipitation, quaking aspen was preferred. In a thermally average year (1997) with low precipitation, black cherry was preferred. Determining whether or not these relationships between localized climate and localized preference are true relationships, or artifacts due to either experimental procedure, low number of butterflies, or another source of variation, is an important priority in continuing this line of research. First, one would have to examine the preferences across years and sites and try to distinguish what, if any, trends exist.

This project indicates that both temperature and precipitation can be important factors influencing plant-herbivore interactions, and subsequently could be important evolutionary selective factors. In addition, responses to varying soil type, and other factors such as geographic variance and photoperiod could be controlled by common garden experiments or other studies. One example would include not only examining oviposition preference of field caught butterflies on field collected foliage, but also butterfly preference on foliage from trees reared in specific conditions. Through this combination of oviposition arrays, one might be able to determine if localized populations exhibit any variance in oviposition preference, or if the differences in oviposition preference are a species-wide response to differences in host plant quality.

My research showed that ash preference of butterflies from the Lower Peninsula 'cold pocket' of Michigan was less than 20% in five choice arenas in 1996 and 1997. This is a decline from the observation of these same populations in 1991 to 1995 that showed ash preferences of 92%, 71%, 60%, 39% and 34% respectively (Scriber 1996a and unpublished). This is especially interesting in view of the increase in seasonal

degree-days observed during this period (e.g. 700, 800, 900, 1000 from 1992-1995; Figure 1) which could allow influx into the 'cold pocket' from surrounding areas, and the survival on most host plants during this period. Since 1991, there were no severely constrained years that could select out non-ash preferring females.

Table 1: Scientific and common names of host plants examined for P. canadensis Table 1: Scientific and common names of host plan
oviposition preference

oviposition preference

Table 2: Accumulated degree-days $^{\circ}$ C (threshold temperature 10 $^{\circ}$ C) at three sites in
Northern Michigan Table 2: Accumulated degree-days °C (threshold temperature 10 °C) at three sites in Northern Michigan

Table 3: Stepwise regression of accumulated degree-days at three sites, 1969-1997			
Regressor	p Value	Contribution to r^2	Remaining in model?
March 1 - October 31			
year	< 0.0001	0.28	yes
site	<0.004	0.15	yes
adjusted $r^2 = 0.34$			
May 1 - July 31			
year	< 0.0001	0.28	yes
site	< 0.004	0.08	yes
adjusted $r^2 = 0.34$			
May 1 - July 5			
year	<0.08	0.06	yes
site adjusted $r^2 = 0.07$	< 0.18	0.04	\mathbf{no}

Table 3: Stepwise regression of accumulated degree-days at three sites, 1969-1997 Table 3: Stepwise regression of accumulated degree-days at three sites, 1969-1997

Table 4: Stepwise regression of water content of leaves of five species collected at Table 4: Stepwise regression of water content of leaves of five species coll
Pellston and Vanderbilt, 1996
A.

Pellston and Vanderbilt, 1996

A.

 $r^2 = 0.42$, adjusted $r^2 = 0.42$

Adjusted for Degree Day Differences, 1996

B.

 $r^2 = 0.42$, adjusted $r^2 = 0.42$

Table 5: Stepwise regression of water content of leaves of five species collected at Table 5: Stepwise regression of water content of leaves of five species coll
Pellston, Vanderbilt and Cross Village, 1997 Table 5: Stepwise regression of water content of leaves of five species coll
Pellston, Vanderbilt and Cross Village, 1997
Regressor: p Value: Contribution to r^2 : Remaining in model? Pellston, Vanderbilt and Cross Village, 1997

			Table 5: Stepwise regression of water content of leaves of five species colle
		Pellston, Vanderbilt and Cross Village, 1997	
Regressor:	p Value:	Contribution to r^2 :	Remaining in model?
Date	< 0.0001	0.35	yes
Site	< 0.0001	0.009	yes
Tree Species	< 0.0001	0.02	
			yes
			Table 6: Stepwise regression of water content of leaves of five species colle
r^2 = 0.38, adjusted r^2 = 0.38		Pellston and Vanderbilt, 1997	
Regressor:	p Value:	Contribution to r^2 :	Remaining in model:

Table 6: Stepwise regression of water content of leaves of five species collected at

Pellston and Vanderbilt, 1997

 $r^2 = 0.32$, adjusted $r^2 = 0.32$

Table 7: Stepwise regression of water content of leaves of five species collected at Table 7: Stepwise regression of water content of leaves of five species col
Pellston and Vanderbilt for 1996 and 1997

			Table 7: Stepwise regression of water content of leaves of five species col
		Pellston and Vanderbilt for 1996 and 1997	
Regressor:	p Value:	Contribution to r^2 :	Remaining in model:
Date	0.0001	0.33	yes
Site	< 0.005	0.0003	yes
Tree Species	< 0.0001	0.008	yes
Year	< 0.0001	0.06	yes

 r^2 = 0.36, adjusted r^2 = 0.36

Table 8: ANCOVA results for 1996 oviposition preference of P. canadensis on five host plant species Table 8: ANCOVA results for 1996 oviposition preference of P. canadensis on five host plant species

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Table 9: ANCOVA results for 1997 oviposition preference of P. canadensis on five host plant species Table 9: ANCOVA results for 1997 oviposition preference of P. canadensis on five host plant species

Table 10: ANCOVA results for 1998 oviposition preference of P. canadensis on young and old (fully expanded) white ash Table 10: ANCOVA results for 1998 oviposition preference of P. canadensis on young and old (fully expanded) white ash

Table 11: ANCOVA results for 1997 oviposition preference of P. canadensis on white ash collected from four sites, resulting in Table 11: ANCOVA results for 1997 oviposition preference of P. canadensis on white ash collected from four sites, resulting in

phenological differences in white ash phenological differences in white ash

Table 12: ANCOVA results for 1997 oviposition preference of P. canadensis on white ash extracts from four sites Table 12: ANCOVA results for 1997 oviposition preference of P. canadensis on white ash extracts from four sites

Table 13: 1997 P. canadensis larval survival in each instar for larvae reared on black Table 13: 1997 *P. canadensis* larval survival in each instar for larvae reared

cherry, paper birch, white ash, basswood and quaking aspen

Source

Denominator df F value

Proposition Table 13: 1997 P. canadensis larval survival in each instar for larvae reared
cherry, paper birch, white ash, basswood and quaking aspen cherry, paper birch, white ash, basswood and quaking aspen

Table 14: Mean and percent differences in pupal weights of P. canadensis reared on black

cherry, paper birch, white ash, basswood and quaking aspen, 1996		
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Values with the same letter are not statistically significant from each other.

Table 15: Mean and percent differences in pupal weights of P. canadensis males and Table 15: Mean and percent differences in pupal weights of P . *canadensis* males and
females reared on black cherry, paper birch, white ash, basswood and quaking aspen,
1997 females reared on black cherry, paper birch, white ash, basswood and quaking aspen,

Values with the same letter are not statistically significant from each other.

Table 16: Mean and percent differences in days until pupation of P. canadensis males and females reared on black cherry, paper birch, white ash, basswood and quaking aspen, Table 16: Mean and percent differences in days until pupation of *P. canadensis* males and
females reared on black cherry, paper birch, white ash, basswood and quaking aspen,
1997

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Values with the same letter are not statistically significant from each other.

Figure 1: Accumulated degree-days at three sites; Cross Village, Pellston and Vanderbilt, 1969-1997. Δ is seasonal (March 1st - October 31st) degree-days; \overline{B} is flight and larval season (March 1st - July 31st) degree-days; C is flight season (March 1st -July 5th) degree-days. Linear trends are illustrated for Vanderbilt data. The trend is statistically significant in \underline{A} ($r^2 = 0.27$, n=29), but not in \underline{B} ($r^2 = 0.18$), nor in \underline{C} ($r^2 = 0.09$).

Figure 2: Heat/ precipitation indices for Vanderbilt, Michigan. May (diamonds), June (squares), July (triangles), and August (circles) 1987-1997. July, 1989 and June, 1991 are extreme outliers.

Figure 3: Percent water content of leaves from five species collected at Pellston (squares) and Vanderbilt (circles). \underline{A} is black cherry; \underline{B} is paper birch; \underline{C} is white ash; \underline{D} is basswood; and E is quaking aspen. Data from the 1996 season.

Figure 4: Percent water content of leaves from five species collected at Cross Village (triangles), Pellston (squares) and Vanderbilt (circles). \underline{A} is black cherry; \underline{B} is paper birch; C is white ash; D is basswood; and E is quaking aspen. Data from the 1997 season.

dotted bars), or collected in the Upper Peninsula (n= 23, cross-hatched bars) for oviposition on leaves of five species, or dotted bars), or collected in the Upper Peninsula (n= 23, cross-hatched bars) for oviposition on leaves of five species, or Figure 5: Preference of butterflies collected in Pellston (n= 31, diagonal striped bars), collected in Vanderbilt (n= 17, Figure 5: Preference of butterflies collected in Pellston (n= 31, diagonal striped bars), collected in Vanderbilt (n= 17, no leaf (paper). Represented means and standard errors of means for any one bar type are adjusted for a balanced no leaf (paper). Represented means and standard errors of means for any one bar type are adjusted for a balanced design. Leaves were from the Pellston area. Data from the 1996 season. design. Leaves were from the Pellston area. Data from the 1996 season.

for oviposition on leaves of five species, or no leaf (paper). Represented means and standard errors of means for any for oviposition on leaves of five species, or no leaf (paper). Represented means and standard errors of means for any Figure 9: Preference of butterflies collected in Pellston (n= 6, diagonal striped bars), collected in Vanderbilt (n = 5, dotted bars), the Upper Peninsula (n=1, cross-hatched bars) and the combined populations (n = 12, gridded bars) dotted bars), the Upper Peninsula (n=l, cross-hatched bars) and the combined populations (n = 12, gridded bars) one bar type are adjusted for a balanced design. Data from the 1997 season. one bar type are adjusted for a balanced design. Data from the 1997 season.

ash, basswood, quaking aspen. (No larvae survived on paper birch.) Data from the 1996 season.

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APPENDICES

APPENDIX A

 $\mathcal{L}^{\text{max}}_{\text{max}}$ and $\mathcal{L}^{\text{max}}_{\text{max}}$

APPENDIX ¹

Record of Deposition of Voucher Specimens"

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens. PPENDIX 1

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viations for table on following sheets:

Voucher No.: 1998-6

Title of thesis or dissertation (or other research projects):

Testing the 'Cold-Pocket' Hypothesis: Oviposition Preference of the Canadian Tiger Swellowtail

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

lnvestigator's Name(s) (typed) Viations for table on following
State University (MSU)
Investigator's Name(s) (typed
Piera Y. Gima
Date 25 Argst, 1998

Piera Y. Gimux

Date 25 Argust 1998

'Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24: 141-42.

Deposit as follows:

Original: Include as Appendix ¹ in ribbon copy of thesis or dissertation.

Copies: Include as Appendix ¹ in copies of thesis or dissertation. Museum(s) files. Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

 $Page_2$ of 2 Pages Voucher Specimen Data APPENDIX 1. ^l

					Number of:			
Species or other taxon	collected or used and deposited Label data for specimens	Eggs	Larvae	Pupae Nymphs	Adults o	Adults σ	Other	Museum where deposited
canadensis Papilio	County, MI V-27-98, Piera Y. Girouk lab reared stock from Dickinson				R			State
	County, MI V-25-1998, Piera Giroux lab reared stock from Dickinson							Entomology
	County, MI V-27-1998, Piera Giroux lab reared stock from Dickinson							University
	Ludington, Mason County, MI V-21-1998, Piera Giroux							Museum,
	County, MI VI-3-1998, Piera Giroux lab reared stock from Dickinson							(MSU)
	County, MI VI-3-1998, Piera Giroux lab reared stock from Charlevoix							Michigan
(Use additional sheets if necessary)								
Giroux Investigator's Name(s) Piera Y.	deposit in the Michigan Signe University Received the above listed specimens for Voucher No. 1998-6							
	Entorpotory Museum,							

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Date 25 August 1998

Date 25 August 1998

Curator

Date

26 aug 1998

APPENDIX B

APPENDIX B

Table 17: Stepwise regression of water content of leaves of five species collected at **APPENDIX B**
Table 17: Stepwise regression of water content of leaves of five species
Pellston and Vanderbilt adjusted for degree-day differences, 19 Pellston and Vanderbilt adjusted for degree-day differences, 1997

		APPENDIX B	
			Table 17: Stepwise regression of water content of leaves of five species
			Pellston and Vanderbilt adjusted for degree-day differences, 19
Regressor:			p Value: Contribution to r^2 : Remaining in model?
Degree-Day	< 0.0001 0.29		yes
Site	< 0.0001 0.007		yes
Tree Species	< 0.0001	0.01	yes
$r^2 = 0.32$, adjusted $r^2 = 0.31$			
			Table 18: Stepwise regression of water content of leaves of five species
			Pellston and Vanderbilt adjusted for degree-day differences, 1996 a

Table 18: Stepwise regression of water content of leaves of five species collected at Pellston and Vanderbilt adjusted for degree-day differences, 1996 and 1997

		APPENDIX B						
			Table 17: Stepwise regression of water content of leaves of five species					
Pellston and Vanderbilt adjusted for degree-day differences, 19								
Regressor:	p Value:	Contribution to r^2 :	Remaining in model?					
Degree-Day	< 0.0001	0.29	yes					
Site	< 0.0001	0.007	yes					
Tree Species	< 0.0001	0.01	yes					
$r^2 = 0.32$, adjusted $r^2 = 0.31$								
Table 18: Stepwise regression of water content of leaves of five species Pellston and Vanderbilt adjusted for degree-day differences, 1996 a								
Regressor:	p Value:		Contribution to r^2 : Remaining in model?					
Degree-Day	< 0.0001	0.32	yes					
Site	< 0.2	0.0003	yes					
Tree Species	< 0.0001	0.008	yes					
Year	< 0.0001	0.06	yes					

 $r^2 = 0.35$, adjusted $r^2 = 0.35$

APPENDIX C

APPENDIX \bullet

Table 19: 1996 Five choice oviposition preference by P.canadensis Table 19: 1996 Five choice oviposition preference by P.canadensis

Mother	Site	Assigned	Leaves	Black	Paper birch White ash		Basswood	Quaking	Paper	Total Eggs
number	Location	Site		cherry				aspen		
P201	Cheboygan		Pellston	30.4	$^{4.3}$	47.8	$_{0.0}$	17.4	$_{0.0}$	
P203	Cheboygan		.0 Pellston	$_{0.0}$	$\overline{0}$	$_{0.0}$	$_{0.0}$	100.0	$_{\odot}$	
P204	Emmet		Pellston	$\overline{0.0}$	100.0	$_{0.0}$	$_{0.0}$	$\overline{0}$	$_{\odot}^{\circ}$	
P205	Emmet		.0 Pellston	32.9	$\overline{0}$	41.4	15.7	$\overline{8.6}$	$\overline{4}$	
P206	Emmet		.0 Pellston	100.0	$\overline{0.0}$	0.0	$_{0.0}$	$\overline{0.0}$	$_{0.0}$	
P212	Emmet		1.0 Osego	75.0	$\overline{0}$	25.0	$_{\rm 0.0}$	$\overline{0}$	$_{\odot}^{\circ}$	
P ₂₁₃	Cheboygan		1.0 Osego	92.7	$\overline{0}$	$\frac{8}{1}$	3.6	$\frac{8}{2}$	$_{0.0}$	
P ₂₁₄	Cheboygan		Otsego	$_{0.0}$	$\overline{0}$	100.0	$_{0.0}$	$\overline{0}$	$_{0.0}$	
P215	Cheboygan		1.0 Pellston	25.6	2.2	55.6	$_{0.0}$	13.3	33	
P219	Cheboygan		.0 Pellston	40.0	$\overline{0}$	33.8	$\overline{13}$	25.0	$_{0.0}$	≅
P222	Cheboygan		1.0 Pellston	41.7	12.5	\overline{a}	20.8	22.9	$_{0.0}$	
P225	Charlevoix		2.0 Pellston	77.8	$\overline{0}$	$\overline{0.0}$	Ξ	Ξ	$_{\odot}$	
P227	Charlevoix		2.0 Pellston	60.0	$\overline{0}$	$_{0.0}$	$_{0.0}$	40.0	$\overline{0}$	
228	Charlevoix		2.0 Pellston	22.6	$_{0.0}$	$_{0.0}$	28.3	49.1	$_{0.0}$	
P230	Charlevoix		2.0 Pellston	16.0	12.0	48.0	9.3	$\frac{1}{4}$	$_{\rm 0.0}$	
P231	Charlevoix		2.0 Pellston	$\frac{8}{11.8}$	$\overline{0}$	20.6	35.3	11.8	20.6	
P232	Charlevoix		2.0 Pellston	$_{0.0}$	$_{0.0}$	$_{0.0}$	100.0	$_{0.0}$	$_{\odot}$	
234	Charlevoix	2.0	Pellston	3.8	3.8	30.8	42.3	15.4	3.8	
P235	Charlevoix		2.0 Pellston	18.8	$\overline{0}$	25.0	37.5	$_{0.0}$	18.8	
P237	Charlevoix		2.0 Pellston	$_{\rm 0.0}$	0.0	$_{0.0}$	$_{\rm 0.0}$	$_{0.0}$	100.0	
P239	Charlevoix		2.0 Pellston	23.1	0.0	76.9	$\overline{0}$	$\overline{\circ}$	$\overline{0}$	

Table 20: 1997 Five choice oviposition preference by P. canadensis Table 20: 1997 Five choice oviposition preference by P. canadensis

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Table 21: 1998 Young and old oviposition preference by P. canadensis

		Table 22: 1997 P. canadensis oviposition preference for white ash collected from four site									
Mother #		Collection	Assigned		Pellston	Vanderbilt	Cross	Okemos	Paper	Total Eggs	
P205		Site Emmet	Site	1.0	32.1	39.2	Village 17.8	10.7	0.0		28
P213		Cheboygan		1.0	0.0	0.0	0.0	100.0	0.0		
P262		Cheboygan		1.0	36.5	7.6	9.6	44.2	1.9		52
P ₂₆₃ P ₂₆₄		Cheboygan Cheboygan		1.0 1.0	26.6 12.9	31.6 33.3	25.0 20.3	15.0 32.4	1.6 0.9		60 108
P ₂₆₆		Cheboygan		1.0	23.0	15.3	46.1	15.3	0.0		13
P ₂₃₀		Charlevoix		2.0	11.1	40.2	27.7	20.8	0.0		72
P242 P273		Charlevoix Otsego		2.0 2.0	11.2 13.1	35.4 26.3	20.9 11.8	32.2 47.3	0.0 1.3		$\overline{6}$ ₂ 76
		Otsego		2.0	20.1	35.0	16.2	25.3	3.2		154
P276 P277		Otsego		2.0	0.0	0.0	00.0	0.0	0.0		
P349 P279		lUP Otsego		4.0 2.0	48 17.3	11.5 30.4	11.5 4.3	28.8 47.8	0.0 0.0		52 23
		Table 23: 1997 P. canadensis oviposition preference for extracts of white ash collec				from four sites					
		Mother Collection Site	Site			Assigned Pellston Vanderbilt Cross Village	Okemos		Water Acetone	Paper Total	
Ł $\overline{P262}$		Cheboygan	1.0	0.0		0.0 33.3		0.0 66.7	0.0	0.0	Eggs $\overline{\mathbf{3}}$
P ₂₆₄		Cheboygan	1.0	13.3		22.2 31.1		17.8 11.1	4.4	0.0	45
P230		Charlevoix	2.0	28.0		4.0 4.0		16.0 12.0		12.0 24.0	25
P273 P360	Otsego	Cheboygan	2.0 2.0	50.0 0.0		50.0 0.0 0.0 0.0	100.0	0.0 0.0 0.0	0.0 0.0	0.0 0.0	$\overline{2}$ $\overline{\mathbf{3}}$
P332	Iron		4.0	50.0		0.0 0.0	50.0	0.0	0.0	0.0	$\overline{\mathbf{r}}$
P 340 P349	I ron I ron		4.0 4.0	7.3 13.9		26.8 17.1 20.8 18.1		22.0 24.4 27.8 15.3	2.4 4.2	0.0 0.0	41 72

Table 22: 1997 P. canadensis oviposition preference for white ash collected from four sites

Table 23: 1997 P. canadensis oviposition preference for extracts of white ash collected

Mother	Date	Host Plant	Pupal weight
#			(g)
P106		7 July 1996 Black cherry	0.9079
P106		7 July 1996 Black cherry	0.7248
P106		7 July 1996 Black cherry	0.7652
P ₁₀₇		15 July 1996 Black cherry	0.7949
P107	20 July 1996 Black cherry		0.8989
P ₁₀₇	21 July 1996 Black cherry		0.8237
P107	21 July 1996 Black cherry		0.8755
P107	22 July 1996 Black cherry		0.759
P ₁₀₇	19 July 1996 White ash		0.9173
P107	19 July 1996 White ash		0.7792
P ₁₀₇	21 July 1996 White ash		0.7781
P107	22 July 1996 White ash		0.7889
P ₁₀₇	23 July 1996 White ash		0.6886
P107	23 July 1996 White ash		0.9493
P107	30 July 1996 White ash		0.7693
P ₁₀₇	30 July 1996 White ash		0.7217
P ₁₀₇		04-Aug-96 Quaking aspen	0.7707
P ₁₀₇		26 July 1996 Quaking aspen	0.8377
P107		29 July 1996 Quaking aspen	1.0304
P ₁₀₇		30 July 1996 Quaking aspen	0.9998
P ₁₀₈		19 July 1996 Black cherry	1.0166
P ₁₀₈	23 July 1996 Black cherry		0.572
P ₁₀₈		25 July 1996 Black cherry	0.6172
P ₁₀₈	27 July 1996 Black cherry		0.7725
P ₁₀₈	19 July 1996 White ash		0.7228
P ₁₀₈	20 July 1996 White ash		0.6648
P ₁₀₈	21 July 1996 White ash		0.6722
P ₁₀₉	10 July 1996 ?		0.7358
P ₁₀₉	17 July 1996 ?		1.0073
P ₁₀₉	19 July 1996 ?		0.7351
P110		23 July 1996 Black cherry	0.7647
P110		26 July 1996 Black cherry	0.8324
P110	27 July 1996 Black cherry		0.5436
P110	31 July 1996 Black cherry		0.6517
P112	30 July 1996 Black cherry		0.6829

Table 24: 1996 P. canadensis pupal weight data

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