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**INTERACTION OF INTROGRESSION FROM *PAPILIO
GLAUCUS CANADENSIS* AND DIAPAUSE IN PRODUCING
"SPRING FORM" EASTERN TIGER SWALLOWTAIL
BUTTERFLIES, *P. GLAUCUS* (LEPIDOPTERA:
PAPILIONIDAE)**

J. Mark Scriber¹

ABSTRACT

The small early "spring form" of the eastern tiger swallowtail butterfly, *Papilio glaucus* has been described from Massachusetts and Illinois in the north, southward all the way into North Carolina. The wing size, shape, patterns, and color all resemble the northern subspecies, *P.g. canadensis*. The possibility was explored that the "spring form" could in fact be a reflection of genetic introgression from the northern subspecies into *P.g. glaucus* populations with laboratory hybrid and back-cross studies between *P.g. glaucus* and *P.g. canadensis* under controlled environments on common foodplants. In addition, morphometric multivariate discriminant analyses of 18 wing characters showed that a *P.g. canadensis* genetic component to the 'spring' form could account for much of the wing pattern, size, and shape. Some environmental effects manifested during the diapause stage could also be involved in wing phenotype determination. Both genetic and environmental influences are likely to be involved in the explanation of the "spring form" *Papilio glaucus* throughout eastern North America.

The eastern tiger swallowtail butterfly, *Papilio glaucus* L., occupies the North American continent from Alaska to Mexico east of the Rocky Mountains and is comprised of four putative subspecies: *P.g. arcticus* Skinner, *P.g. canadensis* Rothschild and Jordan, *P.g. glaucus* L., and *P.g. australis* Maynard (Tyler 1975). The taxonomic status of these 4 entities remains uncertain, although individuals from Alaska (*P.g. arcticus*) and *Papilio glaucus canadensis* populations across Canada and north of the Great Lakes hybrid zone (Fig. 1) are physiologically, ecologically, and morphologically distinct from *P.g. glaucus* and *P.g. australis* (Table 1). In addition, females of *P.g. canadensis* and *P.g. arcticus* lack the Y-linked genetic capacity for the dark (melanic) morph observed in some females of *P.g. glaucus* populations from the Great Lakes Region to southern Florida (including individuals from the purported range of *P.g. australis* [Hagen and Scriber 1989]). Furthermore, all *P.g. canadensis* individuals appear to possess a sex-linked dark color suppressor (S +) which is absent in *P.g. glaucus* and *P.g. australis* (Scriber et al. 1987, Hagen and Scriber 1989). Finally, and perhaps most significant, among the biological differences which set *P.g. canadensis* apart from *P.g. glaucus* and *P.g. australis*, is a gene for obligate diapause in *P.g. canadensis* which also is lacking in *P.g. glaucus*

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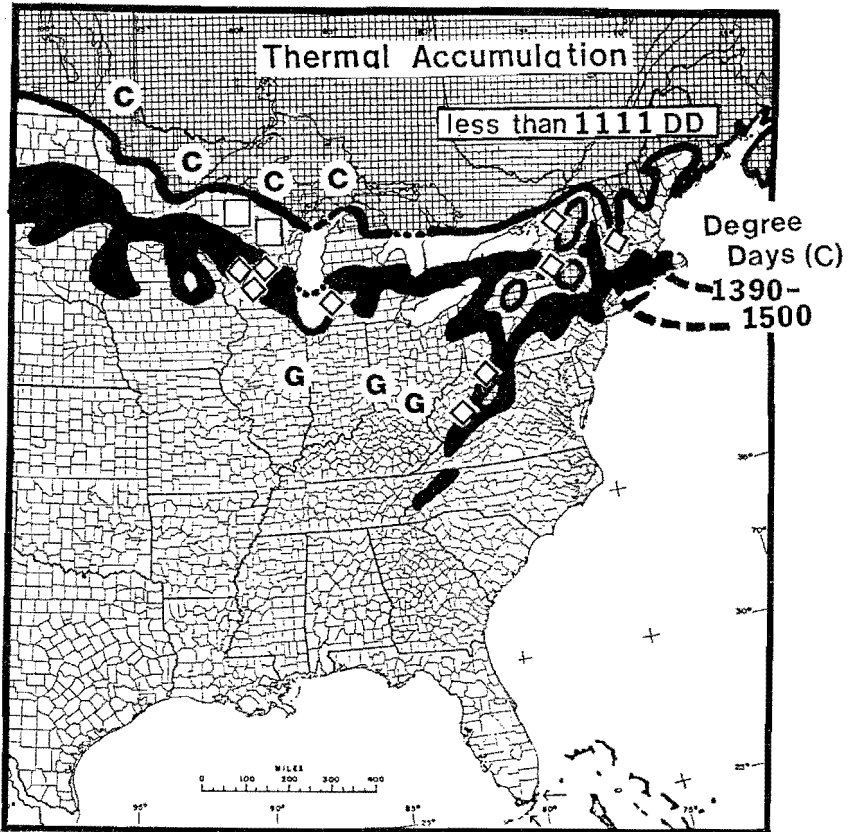


Figure 1. Distribution of selected *Papilio glaucus* populations relative to the seasonal average (20 year) of the thermal unit accumulation above a base threshold of 10°C (50°F) across the Great Lakes and Appalachian Mountain region. The "C" and "G" designate the geographic source of the *P.g. canadensis* and *P.g. glaucus* reference populations used in the multivariate morphometric analyses (see Luebke et al., 1988). The large squares represent 8 counties in northern Wisconsin and the small diamonds represent the potential hybrid populations (all males were computer classified; see Table 2).

and *P.g. australis* (Rockey et al. 1987a, 1987b). It may be that *P.g. canadensis* (which likely includes *P.g. arcticus* [Hagen and Scriber 1990]) warrants status of a separate species (Hagen and Scriber, in prep.).

The northernmost limits to bivoltine populations of *P. glaucus* is delineated by the zone of the thermal unit accumulation between 1390–1500 C degree days above a base temperature of 10°C (2500–2700 F degree days) and also depends upon the particular foodplant (Scriber 1982, Hagen and Lederhouse 1985, Scriber and Hainze 1987). This zone occurs from Minnesota to New England and is characterized by 20 year averages of meteorological data across the eastern half of the United States (see Scriber and Hainze 1987). Within this zone strong selection for univoltinism and obligate diapause would be favored anywhere less than 2500–2600 degree days

Table 1. — Summary of genetic differences between *P.g. glaucus* and *P.g. canadensis*. We are basically convinced that *P.g. arcticus* = *P.g. canadensis* and *P.g. australis* = *P.g. glaucus* (Hagen and Scriber, 1990).

<i>P.g. glaucus</i> trait	<i>P.g. canadensis</i> trait	Mode of inheritance	Reference
1. Ldh 100	Ldh 79	x-linked allozyme	Hagen & Scriber 1989
2. Pgd-100	Pgd-125	x-linked allozyme	Hagen & Scriber 1989
3. Hk fast (110)	Hk slow (100)	autosomal allozyme	Hagen & Scriber in prep
4.	Obligate diapause	single locus recessive?	Rockey et al. 1987a
5. n = 4 fragments (x bal)	n = 3 fragments	x-linked cytoplasmic (mt DNA)	Hagen & Scriber 1989
6. Female melanism		single y-linked locus	Hagen, Smith, Hagen & Smith, in prep
7.	Melanism suppression	single x-linked locus	Scriber et al. 1987
8. One-banded larvae	Three-banded larvae	?	Hagen & Scriber 1989
9. Tuliptree detoxification		2-4 loci? dominant autosomal?	Scriber et al. unpublished
10.	Quaking aspen detoxification	2-4 loci? dominant autosomal?	Scriber 1986
11.	Paper birch detoxification	?	Scriber et al. unpublished
12. Narrow anal wing band	Broad anal wing band	?	Scriber 1988
13. Large adults	Small adults	polygenic?	Luebke et al. 1988
14. Prefers tuliptree for oviposition	Prefers aspen for oviposition	?	Scriber et al. 1990a Scriber et al. 1990b

Table 2. — Multivariate morphometric classification of male *Papilio glaucus* based upon *P.g. canadensis*, *P.g. glaucus*, and hand-paired reciprocal hybrids as reference groups.

Geographic location	Adult flight	Computer classifications (males)		
		<i>canadensis</i>	hybrid	<i>glaucus</i>
8 counties, Northern WI*	(June)	159	1	0
St. Lawrence Co., NY	(June)	7	0	0
Bennington Co., VT	(June)	31	1	0
Madison Co., NY	(June)	5	0	1
Taylor Co., WV	(July)	0	5	2
Clay Co., WV	(July)	0	3	6
Allegan Co., MI	(July)	0	3	2
Green Lake Co., WI (wild)	(June)	8	0	0
Green Lake Co., WI (#1303)	(Late July)	0	5	0
Dane Co, WI**	(July-August)	2	10	62
Richland Co., WI**	(June)	2	5	1

*Bayfield, Washburn, Sawyer, Clark, Wood, Price, Oneida, Marinette.

**Data from Luebke et al., 1988.

obligate diapause would be favored anywhere less than 2500–2600 degree days accumulate because larvae of a second generation would not be able to complete development to the pupal stage before leaf abscission and the onset of winter. On the other hand, there is no obvious reason why *P.g. canadensis* would not be able to

ous effects of warmer temperatures may be involved (Ritland and Scriber, 1985). In fact, the extension of this thermal zone southward in the Appalachian Mountains to Virginia, West Virginia, and Pennsylvania toward the Smoky Mountains may permit introgression of *P.g. canadensis* type genes into adjacent populations throughout much of the mid-latitude regions of the eastern third of the U.S. as well as throughout the Great Lakes Region (Table 2, Fig. 1).

With this possibility of genetic introgression from *P.g. canadensis* over large areas of the U.S. south of Canada, it was of interest to determine whether this might largely explain the occurrence of the morphologically distinct early "spring brood" of various *Papilio glaucus* populations (Clark and Clark 1951, Irwin and Downey 1973, Shapiro 1974, Tyler 1975). The phenomenon of "spring brood" distinctness between the earliest emerging individuals and subsequent summer generations has been previously described in considerable morphological detail (Clark 1932, Clark and Clark 1951). The wing shape, wing size, and many features of wing color patterns are strikingly similar for the early "spring form" of *P.g. glaucus* and for *P.g. canadensis* from Newfoundland to Alaska.

The following is a description of the spring form (Clark 1932):

"... males are very small with the forewings from 42 mm to 45 mm in length. The hair on the thorax and abdomen is very long, and there is a conspicuous tuft of long hair on the frons.

On the upper surface the black border of the hindwings is narrower than it is in the summer form, and the yellow crescents included in it are larger. The black border of the forewings is slightly broader anteriorly than posteriorly, the reverse being true in the summer form, and the yellow spots included in it are larger. The black abdominal border of the hindwing is usually much broader than the interspace between it and the cell.

On the lower surface the dark margin of the hindwings is markedly narrower than it is in the summer form, and its inner border is a straight instead of a scalloped line; it is much more heavily suffused with light scales than it is in the summer form, and the submarginal crescentic spots are very much larger. On the underside of the forewings the submarginal spots in the black border are larger than in the summer form and are usually confluent, forming a rather broad yellow band with a gently scalloped inner border, though they may be separated at the veins."

A comparison photo with details of each morphometric trait measured or scored in this study can be found in Luebke et al. (1988).

After their 1906 description of *Papilio glaucus canadensis* Rothschild and Jordan wrote that the southern spring specimens of *P.g. glaucus* somewhat resemble the small northern form (*P.g. canadensis*), but indicated that the two could be easily distinguished by the much narrower black abdominal border of the hindwings of *P.g. glaucus* (Clark and Clark 1951). Indeed, this black band on the hindwings can provide an accurate means of distinguishing *P.g. canadensis* and *P.g. glaucus* across their zone of hybridization in Wisconsin (see Scriber 1982, 1988), but this single character is not always sufficient to distinguish the subspecies from their hybrids in this zone. However, multivariate discriminant analyses have increased the precision with which correct identifications can be made of the two subspecies and their hybrids (Luebke et al. 1988). Furthermore, in contrast to Rothschild and Jordan's statement, Clark and Clark (1951) point out that the early 'spring form' of *P.g. glaucus* cannot confidently be determined by any single character, including this dark hindwing band.

Although Hagen and Lederhouse (1985) were unable to find significant differences to allozyme frequencies between the 'spring' (early) and 'summer' (late) populations of *P. glaucus* from Ithaca, New York (in the heart of the zone of presumed hybrid interaction), we have noted significant differences in the adult wing characters from 'early' versus 'late' flights elsewhere in the Great Lakes blend zone. In an

attempt to determine if introgression from *P.g. canadensis* rather than a non-genetically based seasonal polyphenism (see reviews by Maudsley 1973, and Shapiro 1984) might be responsible primarily for the production of the 'spring form', a series of laboratory hybrid studies with backcrosses was conducted and multivariate discriminant analyses on several wing characters of the resulting males were used for analyses. Studies of seasonal polymorphism since the 19th century suggested that environmental factors such as temperature and photoperiod might be the "adaptive" cause of the different seasonal morphs in many Lepidoptera (Weismann 1896, see also Oliver 1970, Maudsley 1973, Shapiro 1984).

These studies reported here were designed to elucidate the mechanisms affecting the differential diapause response and eclosion sequence (as well as their potential consequences) in *Papilio glaucus*, especially with regard to the genetic versus seasonal polyphenism alternatives (Müller 1955, Oliver 1970). To determine whether diapause itself (winter conditions) caused the adult wing character differences, or genetic effects from *P.g. canadensis* were involved, controlled environment studies and hybridization studies were concurrently employed.

MATERIALS AND METHODS

Adult females of *Papilio glaucus glaucus* and *P.g. canadensis* were collected from the various field locations (Fig. 1) and allowed to oviposit individually on acceptable foodplant leaves (black cherry and sassafras) kept fresh by water-filled aquapics®. Females were housed in clear plastic boxes (12 cm × 20 cm × 30 cm) heated by a 100 W incandescent lightbulb placed approximately 0.5 m from the boxes. Eggs were removed from leaves after oviposition and neonate larvae were subsequently reared on excised leaves of various species of plants (in 4 cm × 15 cm petri dishes with screened ventilation) to pupation. Larvae were reared in controlled environment growth chambers (at 16:8 photo/scotophase with a corresponding temperature regime of 23.5/19.5°C). Foodplant leaves were kept turgid by use of water-filled aquapics, and changed as needed. A mixture of healthy-looking mature (fully-expanded) leaves and younger leaves were used for neonate studies. After weighing, pupae were individually placed in 14 cm diameter screen cages until adult emergence.

Hand-pairings of lab-reared virgin female butterflies to field-collected or lab-reared males were conducted with the pair hanging in a screen cylinder (approximately 12 cm tall by 14 cm diameter) covered by the top and bottom of a petri dish. Females were subsequently set up in the oviposition boxes as described above and eggs were removed every 2 days. Newly enclosed larvae were individually transferred with a camel hair brush and distributed among the various foodplants and reared to pupation as above. All pupae were allowed to remain under non-diapausing conditions for at least 8 weeks for possible adult eclosion. Pupae that did not produce adults during this time period were stored under refrigeration at 5-7°C until the following spring when they were once again set up for adult eclosion in the screen cages (as above).

Only males were used in these morphometric discriminant analyses because many distinguishing characters are obscured in the melanic (dark) morph of the female *P.g. glaucus*. The reference groups against which these summer- and spring-eclosed adults were run as unknowns were field-captured *P.g. glaucus* (from Illinois and Ohio), field-captured *P.g. canadensis* (from Manitoba, Minnesota, and the Upper Peninsula of Michigan), and various hand-paired laboratory F₁ hybrids (including both reciprocal crosses). Fifteen different wing characters were scored for all individuals and data were analyzed using "Stepwise Discriminant Analysis"—BMDP/PM7 (Dixon and Brown 1979) on a Sperry 1108 computer. Additional details of the methodology can be found in Luebke (1985) and Luebke et al. (1988).

Table 3.—Computer classification based on multivariate morphological analyses of male *P.g. glaucus* captured in two flight periods from the same location in Dane County Wisconsin.

Date of capture	Total (n)	Computer classification		
		<i>P.g. canadensis</i>	"hybrid"	<i>P.g. glaucus</i>
'Spring', May/early June	(5)	4	1	0
Summer, August	(19)	0	9	10

RESULTS

Because southern regions of Wisconsin, Michigan, and New York State represent the northernmost limits of the multivoltine life cycle in *P. glaucus* populations (Rockey 1987a, Scriber and Hainze 1987), it was thought that these areas especially might be likely to reflect genetic introgression from the northern *P.g. canadensis* subspecies manifested in 'spring form' morphology. In fact, southern Wisconsin Counties were shown to have all three multivariate classifications *P.g. glaucus*, *P.g. canadensis*, and hybrids (Luebke et al. 1988). A sampling of selected populations from five states across the putative hybrid zone (as delineated by thermal unit accumulations representing the northern limits to multivoltinism) indicated that "hybrid types" occur at all of these locations (except St. Lawrence County, NY) with increased frequency the closer they are to the dark band (1390–1500 degree days °C) indicated in Figure 1.

Of the five individual males captured in Dane County, Wisconsin in May/June ('spring'), four were classified (relative to the basic reference populations) as *P.g. canadensis* with one classified as a hybrid. In contrast, of the August captures (n = 19) from the same Dane Co., Wisconsin location, ten were classified as *P.g. glaucus*, and 9 were classified as hybrids (Table 3). These samples were too small to permit a general conclusion; however, it is clear that some obvious morphological differences were present in these two time periods at the same location.

To assure a mixture of *P.g. canadensis* and *P.g. glaucus* genes, a hand pairing (#628) of a dark daughter of a female *P.g. glaucus* (Pickens Co., SC) with *P.g. canadensis* (Marinette County, WI) was made, and adult males scored in the multivariate technique described. The direct developing individuals (representing the 'summer' flight) scored nearly entirely as F_1 hybrids (n = 12) with only a single individual classification as a *P.g. glaucus*. Of the four males that diapaused and eclosed the following year ('spring' flight), all were classified as pure *P.g. canadensis* (Table 4).

A series of backcrosses was made and the direct developing ('summer') males were compared to the diapausing ('spring') emerging males (Tables 5 and 6). In the backcrosses of hybrid females to *P.g. glaucus* males (#540, #677) and of *P.g. glaucus* females to hybrid males (#255), all three computer classifications were observed (*P.g.c.*, *P.g.g.* and hybrid). There was, however, a difference in the direct (summer) versus diapausing (spring) emerging males, with a strong tendency toward the *P.g.*

Table 4.—Computer classification based on multivariate morphometric analyses of male hybrid offspring from a pairing¹ (#628) of a female *P.g. glaucus* with a male *P.g. canadensis*.

Emergence time	Total (n)	Computer classification		
		<i>P.g. canadensis</i>	"hybrid"	<i>P.g. glaucus</i>
'Spring' (diapausers)	(4)	4	0	0
Summer (developers)	(13)	0	12	1

¹A dark daughter of a dark female collected in Pickens Co., SC (by Ric Peigler) mated to a male *P.g. canadensis* from Marinette Co., WI.

Table 5. — Computer classification based on multivariate morphometric analyses of male backcross offspring of three pairings¹ of hybrids of *P.g. glaucus* × *P.g. canadensis* with *P.g. glaucus* (female parents are listed first).

Pairing type and brood number	Total (n)	Computer classification		
		<i>P.g. canadensis</i>	"hybrid"	<i>P.g. glaucus</i>
<i>(Pgc × Pgc) × Pgg</i>				
#540 'Spring' (diapausers)	(38)	7	30	1
Summer (developers)	(18)	0	5	13
#677 'Spring' (diapausers)	(18)	7	11	0
Summer (developers)	(15)	0	13	2
<i>Pgg × (Pgg × Pgc)</i>				
#255 'Spring' (diapausers)	(30)	10	20	0
Summer (developers)	(11)	0	10	1

¹#540 is a pairing of a hybrid daughter of a *P.g. glaucus* yellow morph mother from Schuykill Co., PA with a male *P.g. canadensis* (from Marinette Co., WI) with a *P.g. glaucus* male from Grant Co., WI.

#677 is a pairing of a yellow daughter from a cross of a dark *P.g. glaucus* female (reared from a dark mother collected in Clark Co., GA) and a male *P.g. canadensis* (from Marinette Co., WI) with a male *P.g. glaucus* from Adams Co., OH.

#255 is a pairing of a yellow daughter of a yellow female *P.g. glaucus* stock obtained from Schuykill Co., PA and a male hybrid (of a *P.g. glaucus* female from Clark Co., Georgia with a male *P.g. canadensis* from Price Co., WI).

Table 6. — Computer classification based on multivariate morphometric analyses of male backcross offspring of two reciprocal pairings¹ of hybrids of *P.g. glaucus* × *P.g. canadensis* hybrids with *P.g. canadensis*. The female of each pairing is listed first.

Pairing type and brood number	Total (n)	Computer classification		
		<i>P.g. canadensis</i>	"hybrid"	<i>P.g. glaucus</i>
<i>Pgc × (Pgg × Pgc)</i>				
#500 'Spring' (diapauser)	(5)	5	0	0
Summer (developer)	(2)	0	2	0
<i>(Pgg × Pgc) × Pgc</i>				
#555 'Spring' (diapauser)	(18)	15	3	0
Summer (developer)	(0)	0	0	0

¹#500 is a pairing of *P.g. canadensis* daughter (of a mother collected in Jackson Co., WI) with a hybrid male son of a yellow mother from Schuykill Co., PA and a *P.g. canadensis* father from Jackson Co., WI.

#555 is a pairing of a hybrid female daughter (of a yellow morph mother from Schuykill Co., PA and a *P.g. canadensis* father from Juneau Co., WI) with a male *P.g. canadensis* from Price Co., WI.

canadensis classification occurring in the spring (Table 5). Of a total 86 backcross males that diapaused ('spring' flight), 24 were scored as pure *P.g. canadensis*, 61 as F₁ hybrids, and only one as a *P.g. glaucus* (Table 4). In contrast, 44 males direct developed ('summer' flight) and none were classified as *P.g. canadensis*, 28 were classified as F₁ hybrids, and 16 were classified as pure *P.g. glaucus* (Table 5).

Of the *P.g. canadensis* male (and reciprocal, female) backcrosses to F₁ hybrids (#500 and #555), no *P.g. glaucus* types were observed in any emergence class. In cross #555 (female hybrid × *P.g.c.* male) all males diapaused and were scored mostly as *P.g. canadensis* (n = 15), with only three as F₁ hybrids (Table 6). In cross #500 (*P.g.c.* female × male hybrid) two males directly developed and were both

scored as F_1 hybrids, whereas the five diapausing individuals were all scored as *P.g. canadensis* in the multivariate discriminant analysis (Table 6).

DISCUSSION

This study of seasonal polyphenism in the eastern tiger swallowtail, *Papilio glaucus*, documents that 'spring form' populations can very closely approach the northern, univoltine *P.g. canadensis* in wing phenotype. The computer classification of each individual illustrated that early flight *P. glaucus* individuals from certain populations within the Great Lakes transition zone (e.g. Green Lakes and Dane Counties, Wisconsin) score more frequently as *P.g. canadensis*, whereas the summer flight from the identical locations score as mostly *P.g. glaucus* or as hybrids (Tables 2 and 3). A follow-up series of classifications was conducted with various known hybrid and backcross hand-pairings of the two subspecies. In these studies, individual siblings were reared under identical conditions with the same foodplant. Comparisons were made between the direct developing (summer flight) versus diapausers ('spring flight') and in all cases, the 'spring' brood (diapausers) scored more toward the *P.g. canadensis* reference group and the "hybrid" form than did the direct developers (Tables 3-5), although sample sizes were small. The backcrosses with more *P.g. canadensis* genes (Table 6) scored closer to the "*canadensis*" type than the backcrosses with *P.g. glaucus* (Table 5), and it is probable that a significant genetic component exists for the multivariate morphometric classification.

There is a strong correlation of pupal weight and wing length in both subspecies of *Papilio* (Fig. 2). The differential effects of allometric growth of smaller versus larger adults could very well explain some of the computer-classified differences in the 'spring' (diapausing) versus 'summer' (direct developing) forms in this study. Even a transformation to remove most of the effects of size as done by Luebke et al. (1988), may not totally correct for allometric difference. Nonetheless, it seems certain that there are a number of genetically induced (as well as environmentally modified) effects on wing morphology, color, and patterns among hybrids of these *Papilio glaucus* subspecies.

While it can be assumed that the genetic control of morphology and growth is likely to be quantitative (Atchley 1983, Leamy and Thorpe 1984), the segregation of hybrid types and the skewed distribution of individuals toward *P.g. canadensis* with diapause and toward *P.g. glaucus* without diapause may also have an environmental component effect. In other words, the physiological processes involved in diapause or the environment itself may affect the pupae in such a way to significantly alter the survival (Sims 1983) or morphology (color, size, shape, and pattern) relative to their non-diapausing siblings (Müller 1955, Oliver 1970). For example, Maudsley (1973) was able to show that chilling pupae of previously diapausing zebra swallowtail butterflies, *Graphium marcellus* (Cramer) during certain early stages of pharate adult development (inside the pupal cuticle) would usually give a spring form adult, whereas chilling of pharate adults in nondiapausing pupae did not. He concluded that diapause may be a prerequisite to the production of spring form butterflies by low temperature, and hence, the lack of the spring form from any second generation (non-diapausing) adults in any particular season. The reasons for this phenomenon remain unclear.

In addition, it was pointed out that adults from unchilled, diapausing pupae were not significantly different from unchilled non-diapausing pupae (Maudsley 1973). In the study presented here with *Papilio glaucus* none of the pupae were chilled after adult development started inside the pupae (i.e. the pharate stage) and, based on the results from zebra swallowtails described above, the prediction would be that no differences would occur between unchilled pharate adults from diapausing versus non-diapausing pupae (Maudsley 1973). This clearly was not the case. It is however possible that an effect was exerted upon the diapausing pupae before any

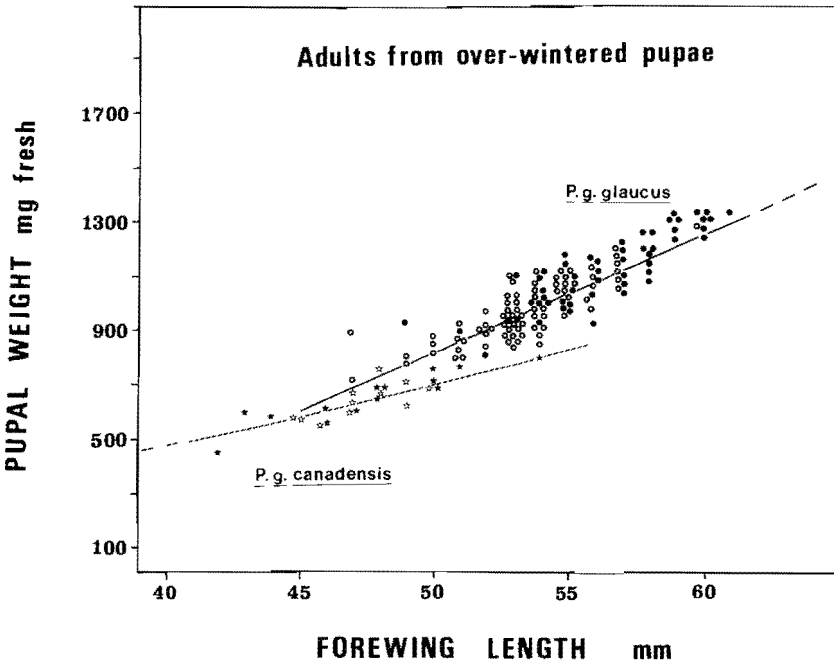


Figure 2. The relationship between adult forewing length (nearest mm) and pupal weight (fresh mass) for *Papilio glaucus* (circles) and *P.g. canadensis* (stars). All individuals were from diapausing stock held at 5–7°C in total darkness for approximately 6 months. Females are indicated by solid black symbols, while males are indicated by open symbols.

of the pharate adult development during the winter (dark) storage period (at 5–7°C). This possibility, and the interaction of temperature and photoperiod cannot be ruled out as influencing the spring brood being skewed toward *P.g. canadensis*, however it has been shown here that there is certainly a genetic component from *P.g. canadensis* itself that will also cause this skewing of the spring brood morphotype of *P. glaucus*.

The adaptive significance of male wing size, shape, and pattern has yet to be shown for either the summer form or the spring form of *Papilio glaucus*, however it is known that *P. glaucus* females can discriminate between and preferentially solicit (Krebs 1988) natural males compared to experimentally painted males (Krebs and West 1988). It is possible that size, shape, color, and color pattern of males combined with mate selection by females may be involved in the maintenance of the *P.g. glaucus/P.g. canadensis* hybrid zone across the Great Lakes region.

It is known that the obligate diapause control gene(s) is located on the sex-chromosome (Rockey et al. 1987b). The directly developing males from backcrosses would totally or partially (heterozygous) lack these *P.g. canadensis* (OD +) gene products (Hagen and Scriber 1989). It could therefore be argued that these individuals would also generally have more *P.g. glaucus* traits, while diapausers would generally have more *P.g. canadensis* traits. The experimental *P.g. glaucus* × *P.g. canadensis* male hybrids from brood #628 should have been comprised of equal complements from the 2 parental genomes. Since it turns out that some of these

diapaused and some did not, and that the computer classification scores these direct developers completely differently than the diapausers (Table 3), it is strongly suggestive that there are also some environmental effects involved here and probably in the field as well.

The specific contributions of genetic versus environmental influences still need to be determined to understand fully the specific causes of the 'spring form' of *Papilio glaucus*. For example, in addition to temperature and photoperiod effects on size of pupae, the particular foodplant and/or its nutritional quality have produced different sized siblings. A single female produced offspring with wing lengths ranging from 40–55 mm on *Populus tremuloides*, from 47–57 mm on *Liriodendron tulipifera*, and from 54–65 mm on *Prunus serotina* (all of which occur from Michigan to New England in this Great Lakes hybrid zone shown in Fig. 1). Since allometric effects can be significant in the classification of morphotypes, and since different pupal/adult sizes result from different hosts, it may be that host plant choice in the hybrid zone and Eastern United States is an important nongenetic variable in the occurrence of 'spring form' *Papilio glaucus*.

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