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EVIDENCE OF LONG RANGE TRANSPORT OF A DARK MORPH SWALLOWTAIL BUTTERFLY (*PAPILIO GLAUCUS*) ON A STORM FRONT INTO NORTHERN MICHIGAN (LEPIDOPTERA: PAPILIONIDAE)J. Mark Scriber¹, Mark D. Deering¹, and Aram D. Stump¹

ABSTRACT

A dark morph female *Papilio glaucus* was captured in the middle of a *P. canadensis* population in the center of Dickinson County, in Michigan's Upper Peninsula. We are unaware of any dark female ever being captured at this latitude, and none within 400 km has ever before been reported. Morphological wing traits all score this dark female as *P. glaucus*, with all 31 of the other (yellow) females captured from the same group of nectar sources scoring as *P. canadensis*. Two diagnostic electrophoretic allozymes (PGD and LDH) show all 24 males to have 100% *P. canadensis* alleles, and 98% *canadensis* alleles were seen for the HK locus. The dark female had the *P. glaucus* X-linked allele for PGD, the *P. canadensis* X-linked allele for LDH, and was heterozygous for diagnostic HK alleles which are autosomal. All other yellow females that were examined were pure *canadensis* type for the sex-linked PGD and LDH alleles. One yellow female was heterozygous for the autosomal HK diagnostic alleles. A long distance "blow-in" on a strong weather front from the southwest is suspected as the most likely explanation for the appearance of this dark morph female of mixed (introgressed) genetic background so far from its nearest known source. The blow-in was not likely to have been in a previous year since this dark morph female would require both (1) a dark morph mother with the Y-linked dark gene and (2) a father that was part *P. glaucus* (i.e. without the color suppressor genes and with a PGD-100 allele). None of the males from this area had PGD or LDH alleles of the *canadensis* type this year or ever previously, making it unlikely that the blow-in occurred in a previous year.

On 25 June 1997, the day after a strong storm with tornado watches blew across Wisconsin and Michigan from the southwest, we captured a dark morph tiger swallowtail (*Papilio glaucus*) female in Dickinson County, of the Upper Peninsula of Michigan. This female, captured nectaring on clover at 11:25 hr, was the largest of 32 females collected at that population site. All other 31 females were yellow and of the *P. canadensis* type, based on key morphometric wing band distinguishing characters (Table 1; and Luebke et al. 1988; Scriber 1990). Dark female morphs are believed to occur only in *P. glaucus* and not in *P. canadensis* (Scriber et al. 1996), and have never before been reported anywhere for the Upper Peninsula of Michigan. This observa-

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Table 1. Wing characteristics of 31 females captured on 25 June 1997 in Dickinson County, Michigan with the dark morph female of *P. glaucus* (see Scriber 1982; Luebke et al. 1988).

	Female color ¹	Forewing length mm ²	Submarginal yellow FW ²	Proportional width % black band anal cell HW ³	Mean class age ⁴
1	Yellow	47	band	65	1.0
2	Yellow	47	band	65	4.0
3	Yellow	49	band	60	1.5
4	Yellow	48	band	60	2.0
5	Yellow	49	band	70	1.0
6	Yellow	47	band	70	1.0
7	Yellow	49	band	85	2.5
8	Yellow	47	band	75	1.5
9	Yellow	48	band	55	1.5
10	Yellow	48	band	75	1.5
11	Yellow	48	band	65	2.0
12	Yellow	51	band	55	1.5
13	Yellow	46	band	55	2.5
14	Yellow	47	band	50	1.5
15	Yellow	52	band	55	1.0
16	Yellow	48	band	80	1.0
17	Yellow	48	band	75	2.0
18	Yellow	46	band	55	2.0
19	Yellow	45	band	80	2.0
20	Yellow	51	band	55	1.5
21	Yellow	48	band	70	1.0
22	Yellow	48	band	70	2.0
23	Yellow	49	band	85	2.0
24	Yellow	49	band	55	2.0
25	Yellow	46	band	50	2.5
26	Yellow	47	band	70	1.0
27	Yellow	48	band	60	2.0
28	Yellow	48	band	65	2.0
29	Yellow	47	band	80	2.0
30	Yellow	48	band	70	2.5
31	Yellow	47	band	65	2.5
32	dark	52	spots	30	2.0

¹ See Scriber et al 1996 (for discussion and genetics of dark morph distribution).

² See Luebke et al 1988 (size can vary according to foodplant reared upon, but has a genetic basis).

³ See Scriber, 1982 (*P. canadensis* usually greatly exceed 50% in band width; *P. glaucus* are usually less than 40%).

⁴ See Lederhouse 1978 (1=perfect, fresh, 4=very worn).

tion is 320–400 km further north than any dark morph female of which we are aware (Fig. 1, Scriber 1996a). From 1978 to 1997, we have previously collected more than 1,100 females of *P. canadensis* in northern Michigan and Wisconsin, and more than 1,200 females of *P. glaucus* in southern parts of these states and adjacent Illinois and Ohio (Scriber 1994, and unpublished).

While dark morph females were reported from Toronto, Canada (Phil

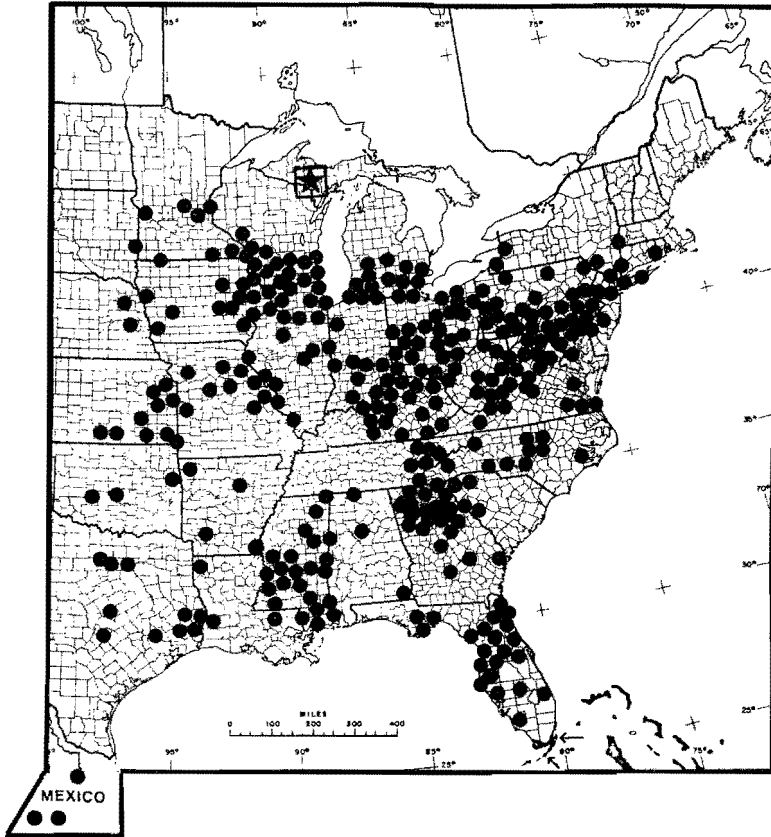


Figure 1. Distribution records more than 4,400 dark morph female *Papilio glaucus* from numerous Museum records and personal collections (modified from Scriber 1996a). The percentage of dark morph females at the northern tier of counties is only 5% Wisconsin, 6% Michigan, and 3% in Massachusetts (Scriber et al 1996). The closest previous county record of any dark morph in Wisconsin is 150–250 miles from our Dickinson County capture site (indicated with a star symbol in the upper peninsula of Michigan).

Schappert, pers. comm.) and Midland, Michigan in the early 1990s (after several of the warmest years on record for the growing season degree-day thermal accumulations), the northward movement of *P. glaucus* genes across the Great Lakes hybrid zone has apparently been minimal and only in the range of 50–100 miles (Scriber and Gage 1995). Nonetheless, the possibility of a relic *glaucus*-type gene pool persisting in this small pocket of several hundred miles out of the geographic range of the species and 400 km from the northern limits of the species' distribution could not be ruled out entirely.

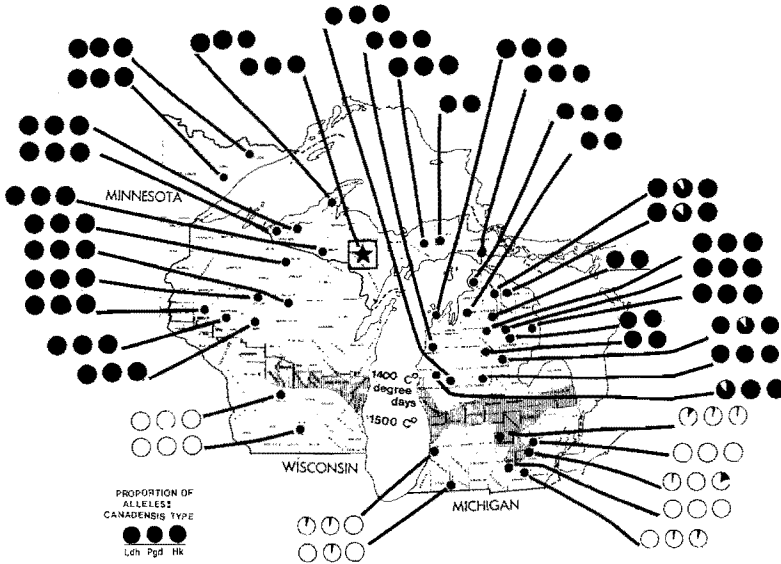


Figure 2. Electrophoretic allozyme frequencies (males only) for LDH, PGD, and HK across the hybrid (transition) zone between *P. canadensis* in the north and *P. glaucus* in the south (modified from Scriber 1996). The shaded region on the map corresponds to the average seasonal total degree day accumulations (1400–1500 degrees C, base 10) that delineate the northernmost limits to bivoltine populations of *P. glaucus*, as well as the previous northernmost limits to dark morph females (see Fig. 1). The Dickinson County dark morph location is indicated with a star (1997 allozyme frequencies of males are presented in Table 2).

Our analyses here consisted of electrophoretic and morphometric comparisons and consultation of weather records to examine the likelihood of relic vs. vagrant *P. glaucus* phenotype and genes.

METHODS

Morphological characters used as potentially diagnostic traits between *P. glaucus* and *P. canadensis* include the wing lengths, submarginal yellow band on the ventral forewings, and the anal cell black band width (Scriber 1982, Luebke et al. 1988, Scriber 1990). Biochemical allozyme electrophoresis differences include hexose kinase (HK), lactate dehydrogenase (LDH), and phosphogluconate dehydrogenase (PGD). Standard techniques were used for enzyme analysis (Hagen and Scriber 1991). Weather data was obtained from the National Weather Service midwest regional data center.

Table 2. Wing characteristics and allozyme alleles of 24 male *P. canadensis* captured in the immediate vicinity of the females (Table 1).

	Forewing length mm ²	Submarginal yellow FW ²	Proportional width % black band anal cell	Alleles** (Allozymes)		
				HW	LDH	PGD
1	46	band	50	110	80	90
2	46	band	70	110	80	90
3	44	band	70	110	80	90
4	44	band	70	110	80	90
5	45	band	80	110	80	90
6	46	band	60	110	80	90
7	46	*band	60	110	80	90
8	46	band	50	110	80	90
9	42	band	60	110	80	90
10	45	band	70	110/100	80	90
11	44	band	60	110	80	90
12	44	band	80	110	80	**90/110
13	45	band	60	110	80	90
14	43	band	70	110	80	90
15	44	band	50	110	80	90
16	43	band	60	110	80	90
17	42	band	80	110	80	90
18	42	band	40	110	80	90
19	44	*band	45	110	80	90
20	44	band	60	110	80	90
21	44	*band	60	110	80	90
22	42	band	70	110	80	**90/110
23	42	band	85	110	80	**90/110
24	47	band	70	110	80	90

*FW submarginal showing some "intermediate" dimpling (see Luebke et al. 1988).

**Both alleles PGD 90 and PGD 110 are *P. canadensis* (see Hagen and Scriber 1989 and Fig. 2).

RESULTS

The 31 yellow females (Table 1), and all of the 24 male swallowtail butterflies we collected in that same area were clearly of the *P. canadensis* type with regard to key morphological wing characters (Luebke et al. 1988).

Hybrid individuals are not always easily identified by a few key wing characters, and we brought the specimens from this population back to Michigan State University to examine for biochemical (allozyme) traits which we have determined to be excellent species diagnostic tools (Fig. 2, Hagen et al. 1991; Scriber 1996a). The results of these analyses showed the 24 males from this population to have 100% of the alleles (PGD-90 and 110 and LDH-80) to be *P. canadensis* type and 97.9% of the HK alleles to be *P. canadensis* type (HK-110; Table 2). One of the males was heterozygous (HK 110/100).

With females, only 18 were able to give excellent allozyme bands for all 3 diagnostic enzymes. The others appear to have lost some stain intensity, perhaps due to the fact that they weakened or died in their oviposition arenas and even with immediate freezing, some enzyme activity was apparently lost

for electrophoretic detection. Every one of the 19 females with LDH stains was the *P. canadensis* type (even the dark morph)! It is interesting that only the dark morph female exhibited the PGD-100 (*P. glaucus*-type) allele of the 20 that exhibited PGD stain. However nearly all the females had *canadensis* alleles, except this dark female and one yellow one that was heterozygous 110/100 for the HK locus of 22 females showing the HK stain. This suggests a complicated genetic scenario for this dark morph female. If the LDH and PGD alleles are sex-linked and fixed (diagnostic) for the two swallowtail species (Hagen and Scriber 1989, 1991; Hagen et al. 1991), then the father of the dark morph female apparently passed an X-chromosome with both *P. canadensis* and *P. glaucus* alleles (suggesting a previous crossover event). This type of male crossover event was once before suggested in a male from a South Manitou Island population from the northern end of Lake Michigan (Scriber 1994). The father of our Dickinson County dark female could also have been *P. glaucus*-like in the HK-100 autosomal allele he contributed.

DISCUSSION

In summary, we have found for this Dickinson County population some evidence of a low level of genetic introgression from *P. glaucus* in 1 male heterozygous for the autosomal HK alleles, and evidence of genetic introgression at the HK locus of 2 heterozygous females including the dark morph, which had one additional *glaucus* allele (PGD). These results are unlike all previous data from the Upper Peninsula in which diagnostic alleles thus far analyzed were clearly *P. canadensis*, without heterozygotes (Scriber 1996a, Scriber et al. 1996, and Fig. 2).

If a pocket of genetically *glaucus*-type individuals existed in this Dickinson County, Michigan population, we would have expected some morphometric traits to clearly be evident in both males and females, but they were not. Furthermore, unless the nationwide pattern of dark/yellow morph female inheritance is inaccurately understood, we should see a dark morph female only if 1) her mother was also dark (since it is a Y-linked trait) and 2) her father was homozygous or heterozygous for the "enabler" gene, or for lacking the "suppressor" gene on the X-chromosome (Scriber et al. 1996). In other words, this dark female required both a dark morph mother and a father that was partly *P. glaucus*, both of which are highly unlikely based on the total lack of dark morphs ever seen in the Upper Peninsula and the large number of morphological/biochemical analyses of the males that were *P. canadensis*-like in this population.

The uncommon and unexpected appearance of dark female daughters from yellow *P. glaucus* mothers can be explained fairly easily, and in most cases it was likely that the yellow mother was carrying the dark allele on her Y-chromosome (Clarke and Sheppard 1962) with a "suppressor" (or lack of "enabler") on her X-chromosome (Scriber et al. 1996). These cases historically are almost always from parents close to the Great Lakes hybrid zone where genetic introgression is most likely (250–300 miles from our dark morph Dickinson Co. female). In contrast, while the appearance of any dark morph daughters from a *P. canadensis* mother has never been reported from nature, it has occurred in one interspecific hybrid brood from our lab studies (Scriber and Evans 1986). In this case a yellow *P. canadensis* female from northern Wisconsin produced 21 dark and 12 yellow (2/3 dark) daughters (male mate was an aberrant colored *P. glaucus* from Ohio). In this exceptional brood (#1132; Scriber and Evans 1986) it could not be resolved as to whether the rare dark daughters were the result of a cross-over event from the Y-chromo-

some or due to a nondisjunction of the sex chromosome (Clarke et al. 1976, and C.A. Clarke, pers. comm.). While we now have evidence that crossovers on the X-chromosome of male *P. canadensis/glaucus* hybrids have occurred in nature (Scriber 1994), and that introgression from *canadensis* may explain "spring form" *glaucus* that look like *canadensis* (Scriber 1990), the cause of the occurrence of dark females from a *canadensis* mother has never been resolved. Therefore, this female dark morph found in Dickinson County could not automatically have been assumed to be a "pure" *P. glaucus* individual. In fact, we have observed that this dark female has the *P. canadensis* sex-linked allele (LDH-80) as well as being heterozygous for the HK diagnostic locus.

The pattern of sex-linked diapause physiology which we have documented for *P. glaucus* and *P. canadensis* (Rockey et al. 1987) clearly indicates that Dickinson County, Michigan has insufficient degree-days of thermal unit accumulation to ever support two generations of *Papilio* (even on the most nutritious host plant species; Scriber and Lederhouse 1992). This area also is near a large "cold pocket" which further shortens the growing season and which has apparently selected for pupation at small weights (Ayres and Scriber 1994) resulting in smaller adult females (as observed in forewing lengths that in this vicinity are generally less than 50 mm Scriber 1994, 1996b and Table 1). The total average growing season degree-day accumulations of thermal units (To > 10°C) for this site in central Dickinson County is only 1000 (Eichenlaub et al. 1990). In one year out of 10 it is only 830, which is barely enough for even a single generation of *P. canadensis* to be completed (Scriber and Lederhouse 1992). Unfortunately, we couldn't assess the obligate diapause trait nor sex-linked oviposition preferences because our dark morph female did not lay any eggs.

Long range transport of insects is believed to occur for other Lepidoptera, and the black cutworm (*Agrotis ipsilon*) reaches the northern Great Lakes and Canada on winds from the Southwest in mid-June (Showers 1977). This is about the same time of the year as this dark female *Papilio* was discovered. It has been suspected during the 1980s that 1st instar ballooning gypsy moth larvae (*Lymantria dispar*) were blown into Wisconsin westward across Lake Michigan (Wisconsin Department of Agriculture, pers. comm.), but convincing evidence is still lacking. Two day-flying *Callosamia promethea* moths (Saturniidae) were marked and recaptured in 3 days at 14 km and 36 km (both upwind, Toliver and Jeffords 1981). Hurricanes have apparently brought several tropical species into Texas (Neck 1978). However, to our knowledge, nothing as large as this female tiger swallowtail has been documented blowing in for distances 400–480 km (Gatehouse 1997), as we think is likely here. The arrival of monarch butterflies in Great Britain has been attributed to hurricanes assisted by the jetstream (Coombs and Tucker 1995). National Weather Service data for 23–25 June in northern Wisconsin and northern Michigan showed winds from the southwest sustained at 16–32 km/h and gusting to 25 mph or higher for nearly 2 days. Winds were sustained at 19–37 km/h for all day 24 June and 25 June (more than 30 hours continuously, with gusts to greater levels) for weather reporting locations in Wisconsin south and southwest of Dickinson County (Appleton, Eau Claire, Greenbay, Wausau, and Rhinelander). Air temperatures were continuously well above that required for *Papilio canadensis* flight (Lederhouse et al. 1995). The temperatures were above 32°C at Eau Claire all afternoon 23 June and were in the 30–32°C range throughout northern Wisconsin on both 23 and 24 June 1997. This front crossed the northern end of Lake Michigan and blew through Pellston, Michigan in the morning of 24 June with temperatures in the 32–34°C range and winds sustained at 16–33 km/h (gusts to 49

km/h) all day on 25 June (NOAA/National Weather Service from NWS and FAA sites; courtesy of Dr. F.V. Nurnberger, MSU State Climatology Program).

Tiger swallowtail butterflies (both *P. canadensis* and *P. glaucus*) have been tracked (by automobile) flying continuously at 16–20 km per hour for distances up to 3 km (JMS pers. obs.). However, extensive marking/release/capture studies in northern Michigan (Charlevoix, Emmet, and Cheboygan counties) and Highlands County, Florida have failed to ever detect movements of individuals greater than 11 km. In some populations daily reciprocal local movements of 2 km have occurred frequently (Scriber et al. 1998 and unpublished). We therefore think it is unlikely that normal flight, even for strong fliers such as *P. glaucus*, could account for the Upper Peninsula arrival of this female in such excellent shape. However, a straight sustained, unidirectional flight of 19 km/h for several hours a day on strong winds could theoretically get her to Dickinson County in only 5–6 days from the closest known record of a dark morph female occurrence.

Our conclusion is that this dark female capture was the result of a blow-in from the strong, sustained, severe weather front that went through rapidly during the previous 36 hours. Her father had to be largely *P. glaucus* and her mother had to have the Y-linked dark morph trait. The Wisconsin hybrid zone seems to be the most likely source of this Dickinson County dark female. Although most individuals are *P. canadensis*-like, dark morph females and introgression from *P. glaucus* have been previously observed in Marquette County and Green Lake County females in central Wisconsin (Scriber et al. 1996). Males from these Wisconsin counties have also exhibited heterozygosity for suppressors and reflect genetic introgression as well. The total absence of dark morph females within 400 km during the last 100 years of collections, and the strong *P. canadensis*-type alleles in all males tested from this area make the possibility of a refugium for *P. glaucus* highly unlikely, favoring the strong wind “blow-in” hypothesis.

We would appreciate comments and information from readers about their observations of northern distribution records for *Papilio glaucus* dark morph females, especially from Minnesota, Wisconsin, Canada, and Michigan.

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