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A Black Phase Female in the Historical Breeding Range of Canadian Swallowtails (Lepidoptera: Papilionidae)

Goran E. D. Blomberg¹ and Edward Herig, Jr.²

Abstract

A black phase female, collected in 2000 in Isabella Co., MI, in the historical range of *Papilio canadensis* Rothschild and Jordan, could be a result of recent introgression by *P. glaucus* L. If so, black females may become widespread, though infrequent, in the northern Lower Peninsula.

A black phase female swallowtail in Michigan State University's entomology museum, was captured alive on the Central Michigan University campus, Isabella Co., 10 May 2000, by Mr. Edward Herig, Jr. (EH). Nielsen (1999) showed this county to be occupied solely by Canadian swallowtails (*Papilio canadensis* Rothschild and Jordan). The location is well within the historical breeding range of presumably purebred *P. canadensis*, being roughly 44 km (27 mi) north of the historical zone of hybridization between this species and the eastern tiger swallowtail (*P. glaucus* L.) (Scriber 2002). Scriber, Hagen, and Lederhouse (1996) show Isabella Co. as within range of 0 % black phase females. That black females occur in *P. glaucus*, but not in *P. canadensis* was implied or stated by Rothschild and Jordan (1906), Clark and Clark (1951), Brower and Brower (1962), and Daniels (2005). (Rarely, "somewhat melanic" individuals of *P. canadensis* are reported, however (Daniels 2005).)

The geographical distribution of the W-linked melanism gene (b+) and the Z-linked enabling factor (s-) has been described (Scriber et al. 1996). The W-linked gene b+ is very slow to move forward via genetic introgression, while the Z-linked s- appears to move more freely northward (Scriber 2011).

Discussion

Four possible causes of a live capture of the specimen (Fig. 1) are that it (1) is a mutant, (2) strayed from the hybrid zone or farther south (over 40 km), (3) was blown in by persistent southerly winds, and (4) reflects recent introgression of *P. glaucus* genes into the historical range of *P. canadensis* of Michigan's Lower Peninsula (LP). Because black phase females in *P. canadensis* have never been reported, the first cause appears unlikely. The second cause seems unlikely in light of Scriber et al. (1998) reporting that intensive marking/release/recapture studies in northern Michigan and in Florida (Highlands Co.) have failed to produce distances greater than 11 km (7 mi).

The third and fourth possible causes merit more discussion. The date of capture (10 May 2000) supports the possibility of the specimen having been blown in. Dr. J. Andresen in the Department of Geography, MSU (2011, pers. comm.), reported persistent southerly winds through mid-Michigan during 4-7 May 2000. Said winds became stronger the two following days, and perhaps

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Figure 1. Black phase female of probable *Papilio canadensis* X *P. glaucus*, captured on the Central Michigan University campus, Isabella Co., MI, 10 May 2000, by Mr. Edward Herig, Jr.

more importantly, preceded the passage of a cold front through the LP late 9 May and on 10 May. Scriber et al. (1998) reported a dark phase female from Dickinson Co. in Michigan's Upper Peninsula in a population of *P. canadensis* on 25 June 1997. To their knowledge, no dark phase female had been captured at this latitude before, and none within 400 km (250 mi) had ever been reported. They reasoned that the specimen was most likely a blow-in, on a strong southwesterly weather front that began two days earlier in Wisconsin. The last possible cause, recent introgression of *P. glaucus* genes into the *P. canadensis* population of the northern LP, is supported by two forms of evidence (Scriber 2002): (1) A northward movement, during 1998-2001, of alleles enabling caterpillars in the LP's historical breeding range of *P. canadensis* to detoxify leaves of tulip tree (*Liriodendron tulipifera* L.), even though this tree species has not expanded its range northward, and (2) a decrease in the mean percentage widths of the abdominal black borders of the hind wings (measured from edge to origin of Cu₂). He reported mean widths of 67% (n = 448) for *P. canadensis* (Dickinson Co.) and 23.2% (n = 35) for *P. glaucus* (St. Joseph Co.). In Isabella Co., from 1998 to 2000, the mean width for the former species had decreased, 58.9 % (n = 50) to 52.4% (n = 34). He reported similar decreases for Leelanau Co. and Benzie Co., from 1999 to 2000. It is reasonable to assume that the W-linked allele, b+, that confers blackness on females, has simultaneously moved northward, granted that it is infrequent, and that its expression is normally suppressed by a Z-linked allele, s+, in the *P. canadensis* population. EH found the specimen in a very fresh condition, with the wings still being soft, and therefore believes it eclosed from a nearby tree. Furthermore, the specimen, after being caged, failed to lay eggs; this suggests that eclosion was too recent to provide a chance to mate. Thus, we believe it more likely to be a local, hybridized *P. canadensis*,

than a blow-in. However, it is also possible that a mated dark phase *P. glaucus* female may have flown to, or more likely was blown into this area the previous summer, laid eggs, and the resultant offspring may have included the specimen caught here. A similar example, from 1999, is a *P. glaucus* male appearing in Charlevoix Co. (roughly 180 km (112 mi) further north); it mated with a *P. canadensis* female that was collected. Her offspring, reared in a laboratory, were hybrid-like in many ways (Donovan and Scriber 2003).

Unfortunately, the reported specimen's taxonomic status cannot be determined by measurements of the forewing, specifically from the origin of the front edge to the ends of veins R4, Cu1, and Cu2. There appears to be no real difference, in Table 1, between respective means of these measurements for females of *P. canadensis* and of females of early *P. glaucus*. Each measurement of the reported specimen, respectively 4.80, 3.55, and 3.40 cm, closely coincides with its respective mean plus standard error of the latter species; differences are at most 1%. Genetic testing of the specimen for hybrid status seems desirable. Because the specimen is dry, however, extraction and detection of the three critical allozymes, LDH, PGD (Z-linked), and HK (somatic) (Scriber et al. 1998) is precluded. The remaining possibility (not attempted) would be detection of mitochondrial DNA (mtDNA) from a male *P. canadensis*. This paternal "leakage", at fertilization, has been reported in butterflies (Gompert et al. 2008), and possible evidence thereof was reported for *P. glaucus* (Andolfatto et al. 2003). It is nevertheless believed to be unusual in insects (Avisé 1989, Sperling 1993, Hurst and Jiggins 2005), and normally only a female's mtDNA is passed on to the next generation. Any attempt to find paternal mtDNA (from some dry body part) will likely not be rewarded. It should be noted that (1) the allele b+ (confers blackness) is W-linked, and therefore is passed on only by females (the heterogametic sex), to female offspring, and (2) a black hybridized female has allele s- on her single Z chromosome (not s+, evidence of a male *P. canadensis* ancestor); therefore, with no paternal leakage, hybrid status via examination of mtDNA cannot be established for the specimen.

Assuming that the reported specimen is a local hybridized *P. canadensis* and a result of the reported introgression, as we believe, we speculate that black females, even if they become widespread in the LP's historical range, are expected to remain at low frequency, for the following reasons: (1) Most or all introgression must be attributed to the early (more contemporary) flight of *P. glaucus*, in which perhaps only 1% of the females are black (while roughly 5% of what are presumably late flight females in Ingham Co. and Clinton Co. are black (Scriber et al. 1996), and lower proportions of black females in the early flight were reported for the District of Columbia by Clark (1932) and for West Virginia by Scriber et al. (1996, citing Thomas Allen (1992, pers. comm.)), (2) According to Scriber et al. (1996), obligate diapause has been strongly selected for in *P. canadensis* (while *P. glaucus* is bivoltine), and is closely linked to the allele s+, on the Z chromosome, that suppresses the expression of the W-linked allele, b+ (confers blackness); this means low frequency of crossovers between the two Z-linked loci in heterozygous males, and therefore a low proportion of daughters having a Z chromosome containing allele s- (passive, or enabling expression of blackness, when b+ is present) linked with obligate diapause, (3) Aside from the close linkage of the suppressor allele, s+, with obligate diapause, it is believed that introgression by s- into the population will only slightly reduce the proportion of its suppressing counterpart, (4) In the *P. glaucus*-*P. canadensis* hybrid zone the unpalatable pipevine swallowtail (*Battus philenor* L.), model for black (mimetic) females, becomes rare or absent (Burns 1966, Scriber et al. 1996, Daniels 2005); it is believed that blackness in females confers little or no selective advantage there and farther north, and (5) The expectedly infrequent black females, even if widespread geographically, will be at a reproductive disadvantage if males, as anticipated, will preferentially mate with yellow females (Brower and Brower 1962, Burns 1966, Scriber et al. 1996).

Table 1. Means and standard errors of measurements (cm) to the ends of selected veins in forewings of females of Canadian swallowtails and eastern tiger swallowtails. Numerals in parentheses denote number of specimens.

Vein	<i>Papilio canadensis</i> ¹	early <i>P. glaucus</i>	late <i>P. glaucus</i>
R4	4.47 ± 0.042 (57)	4.65 ± 0.12 (16)	5.29 ± 0.048 (15)
Cu1	3.40 ± 0.033 (57)	3.51 ± 0.082 (16)	3.96 ± 0.043 (16)
Cu2	3.22 ± 0.031 (57)	3.28 ± 0.087 (16)	3.71 ± 0.036 (16)

¹No measurements from specimens caught during or after 1998, in the LP, are included.

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