AN UPDATE ON TIGER SWALLOWTAILS IN ONTARIO

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Tiger swallowtail is a collective term used to describe several North American butterfly species featuring a yellow ground colour with distinctive black stripes. Two tiger swallowtail species occur in Ontario. The Canadian Tiger Swallowtail, *Papilio canadensis* (Rothschild & Jordan 1906), is found in northern and eastern Ontario while the Eastern Tiger Swallowtail, *Papilio glaucus* (Linnaeus 1758), is found in southern Ontario. These two species are very similar in outward appearance and historically, *P. canadensis* was thought to be a subspecies of *P. glaucus*. Prior to the utilization of molecular and genetic tools in taxonomy, species were defined primarily by observables such as wing pattern, flight times, host plant usage, etc. It is not difficult to see how these two very similar tiger swallowtail species could be classified as one. With advancements in technology and a better understanding of their life histories, it eventually became apparent that although these taxa look similar, they demonstrate consistent and significant differences, prompting the elevation of *P. canadensis* to full species status in 1991 (3).

For example, although both *P. canadensis* and *P. glaucus* can use black cherry (*Prunus serotina* Ehrhart 1784) and white ash (*Fraxinus americana* Linnaeus 1753) as larval host plants, *P. canadensis* strongly prefers quaking aspen (*Populus tremuloides* Michaux 1803) throughout its range while *P. glaucus* larvae essentially cannot survive on this host. Conversely, *P. glaucus* strongly prefers tulip tree (*Liriodendron tulipifera* Linnaeus 1753) and hoptree (*Ptelea trifoliata* Linnaeus 1753) as hosts, but essentially, these cannot be used by *P. canadensis*. When presented with 3-way choice tests in the laboratory using tulip tree, black cherry and quaking aspen, *P. glaucus* shows a strong preference for ovipositing on tulip tree and *P. canadensis* strongly favours ovipositing on quaking aspen (9). Subtle wing pattern and shape differences are also seen between these two species which are discussed in more detail below.

In terms of overwintering, *P. canadensis* exhibits obligate diapause, meaning that there is one generation per year and larvae will enter diapause regardless of environmental conditions. However, *P. glaucus* exhibits facultative diapause, meaning that environmental conditions during the later stages of larval development (4th and 5th instars) dictate whether the resultant pupa will enter diapause (7). If late instar larvae of *P. glaucus* experience relatively long daylight length, the resultant pupae will develop directly into adult butterflies that emerge later that season. As daylight length decreases, a higher proportion of larvae will produce pupae which diapause and emerge as adults the following year. Somewhat surprisingly, temperature does not play a significant role in diapause determination (7).

With *P. canadensis* now recognized as a species in its own right, an interesting question arises: how do *P. canadensis* and *P. glaucus* interact where their ranges meet in southern Ontario and New England? For most biologically distinct species, no interbreeding occurs due to a variety of isolating mechanisms. However, these taxa are very closely related and hybridization can and does occur. This hybrid zone between *P. canadensis* and *P. glaucus* varies in width and shape depending on altitude, latitude and local microclimates, but has historically ranged from 41 to 44°N. In southern Ontario, this maps approximately to the Carolinian zone with the northern limit of *P. glaucus* occurring probably around the Greater Toronto Area. Over the last 3 decades, climate change and milder winter conditions have caused this hybridization band to move north by approximately 40 km, and simulation models show that a northward shift of 55-144 km can be expected per 1°C of warming (6).

Within this hybrid zone, there is a complex set of incompletely understood interactions including, but not limited to, climate, genotypic variation, mating preferences, host plant selection, and diapause characteristics. It is beyond the scope of this introductory article to detail our current understanding of these factors, but for the interested reader, a list of important references has been provided. For the typical amateur butterfly enthusiast, the most relevant and immediate consideration is how to differentiate *P. glaucus*, *P. canadensis*, and their hybrids in the field, based on factors such as location, flight times, wing pattern, and larval traits.

While subtle, there are a number of wing pattern differences between *P. canadensis* and *P. glaucus*. In Figure 1 (see back cover), the specimen on the left is a male *P. canadensis*, obtained from an egg found on quaking aspen in Montebello, QC on June 18 (and subsequently raised on quaking aspen). The specimen on the right is a male *P. glaucus* captured in Hamilton, ON on June 16. The middle specimen is a male hybrid raised from an egg found on black cherry on July 17 in Kingston, ON. Notice the larger size, more pronounced scalloping of the hindwing margins, and deeper yellow colour when *P. glaucus* is compared with *P. canadensis*.

Many of the diagnostic differences between these taxa are actually better seen on the underside. In Figure 2 (see back cover), the sizes of the specimens are not to scale in relation to each other. Proceeding from left to right, the first specimen is a female *P. canadensis*, captured just west of Edmonton, AB on June 15. The second specimen is a female *P. canadensis* from a 3rd instar larva found on chokecherry (*Prunus virginiana* Linnaeus 1753) on July 11 just north of

Kingston, ON. The third specimen is a hybrid female *P. canadensis* from an egg found on black cherry on July 17 in Kingston, ON. The last specimen is a female *P. glaucus* captured in Hamilton, ON on August 1.

Several features are noteworthy, as outlined by boxes 1-3. Box 1 shows a row of submarginal yellow spots on the front wing underside, which form a solid contiguous band in *P. canadensis* but are discrete lunules in *P. glaucus*. Box 2 shows the blue/black band on the hindwing underside, which is straight (or nearly so) in *P. canadensis* but scalloped in *P. glaucus*. Finally, box 3 shows the black band along the anal margin of the hindwing underside, which is much broader in *P. canadensis* than *P. glaucus*. Relative to the width of the entire cell containing the band, it is approximately 10-40% wide in *P. glaucus* and 55-90% wide in *P. canadensis* (12). Overall, the width of this black band is greater in females than males, but the relative difference between species persists (3). All these traits demonstrate variable intermediacy in hybrid specimens. Additionally, the interpretation of these findings should be tempered by the fact that spring brood *P. glaucus* specimens from the northern limit of its range can demonstrate *P. canadensis*-like traits (8), which is influenced by both genetic and environmental factors.

In the extreme southern tip of Ontario, one may rarely encounter a melanic form of *P. glaucus* which has a black ground colour with blue suffusion on the upper surface of the hindwings. This form is only seen in *P. glaucus* females, which are thought to mimic the distasteful Pipevine Swallowtail (*Battus philenor* Linnaeus 1771), another rare species occasionally seen in southern Ontario. Other than sporadic aberrations, melanic females are not known from *P. canadensis*. Intermediate individuals can be seen in the hybrid population (10).

Early instar larvae of these taxa are also different. In Figure 3 (see back cover), the larva on the left is *P. canadensis* from Edmonton, AB on quaking aspen. The larva on the right is *P. glaucus* from Hamilton, ON on tulip tree. The middle larva is a hybrid from Kingston, ON on chokecherry. All these larvae are in their 1st instar. Notice that the *P. glaucus* larva has a white saddle on its dorsal mid section while the *P. canadensis* larva has this saddle as well as anterior and posterior white bands. Hybrid larvae demonstrate reduced anterior and/or posterior white bands, such as the one depicted in the middle photograph.

The known ranges of Ontario tiger swallowtail species may also assist in their identification. South of a line from Hamilton to the southern edge of the Bruce Peninsula, pure *P. canadensis* is unlikely to be encountered, and any tiger swallowtail seen will be *P. glaucus* or *P. glaucus* with some genetic influx from *P. canadensis*. North of this line to the Greater Toronto Area, anything ranging from pure *P. canadensis* to pure *P. glaucus* may be seen, and it may sometimes simply be impossible to assign a definite identity to a specimen, especially if it is not captured and closely examined. Relying on location and flight times alone is not sufficient. North of the GTA to the Ottawa valley, it is unlikely to encounter pure *P. glaucus*. Based on historical climate data, north of this zone, the season is not long enough to support two generations of *P. glaucus* (11). If *P. glaucus* did exist in this region, any adults which emerge in May/June would give rise to larvae ready to pupate by mid summer. Without environmental cues to trigger diapause (they do not exhibit obligate diapause like *P. canadensis*), these pupae would develop directly into adult butterflies, leading to a second generation of *P. glaucus* larvae. Since the growing season is not long enough to allow this second generation to reach the pupal stage (or only rarely), there would be intense selection pressure against *P. glaucus*. Thus, north of the GTA, we find *P. canadensis* or their hybrids.

Some sources state that north of the GTA region, a fresh tiger swallowtail seen in July or August can be considered *P. glaucus*, but this is not consistent with current research. These are late emerging hybrid tiger swallowtails and not a true second generation of *P. glaucus*. Consider fresh tiger swallowtails in July – there simply hasn't been enough time for eggs laid in late May and June to have completed their life cycle yet to produce the July adults. In the literature, this has been termed a "false second generation" or "late flight" (LF) hybrid swarm (2, 11). The "early flight" (EF) tiger swallowtails emerging in May/June are *P. canadensis* with little to no genetic introgression from *P. glaucus* while the LF butterflies are hybrids. The latter also has only one generation per year, like *P. canadensis*, and produce offspring which overwinter and produce the LF adults of the subsequent year (Dr. Mark Scriber, pers. comm.). In Figure 2 (see back cover), the second specimen from the left is an EF *P. canadensis* with no definite *P. glaucus* traits. The third specimen from the left is a LF hybrid *P. canadensis*; notice the narrow black band along the anal margin of the hindwing, which is a *P. glaucus* trait.

Studies on the EF and LF adults have demonstrated differences in ovipositing preferences and ability to use different larval host plants (4). The LF hybrid adults favour laying eggs on tulip tree or hoptree when available, like *P. glaucus*. However, north of the GTA where these host plants are not often encountered (rarely planted as ornamentals), LF adults will typically lay eggs on white ash or black cherry. Hybrid larvae demonstrate survival on tulip tree, unlike pure *P. canadensis*, but this survival rate is lower than that of pure *P. glaucus*. Similarly, hybrid larvae also demonstrate survival on quaking aspen, unlike pure *P. glaucus*, but this survival rate is lower than that of pure *P. canadensis* (4). It is interesting to note that in the field, hybridization between *P. glaucus* and *P. canadensis* is not symmetric. Field experiments in Michigan and Florida have shown that both male *P. glaucus* and *P. canadensis* prefer to mate with female *P. glaucus* (1), although the reasons for this remain unclear. Yet, genetic analyses of these hybrids have found only *P. canadensis*-like mitochondrial DNA, suggesting that genetic introgression likely occurred via hybrid males mating with *P. canadensis* females (5). Future observations and further genetic/molecular studies will be needed to determine the exact nature of gene flow and degree of reproductive isolation between the LF hybrid population and EF *P. canadensis* in eastern Ontario.

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Figure 1. Dorsal views of *P. canadensis* (left), hybrid (middle), *and P. glaucus* (right).

Figure 2. From left to right, ventral views of *P. canadensis*, early flight *P. canadensis* from within the hybrid zone, late flight *P. canadensis* from within the hybrid zone, and *P. glaucus*.

Figure 3. First instar larva of *P. canadensis* (left), hybrid (middle), and *P. glaucus* (right).