

## MORE ON ONTARIO TIGER SWALLOWTAILS

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Two species of tiger swallowtails, Canadian (*Papilio canadensis*) and Eastern (*P. glaucus*), are typically depicted as occurring in Ontario. However, the exact distribution, identification and supposed hybridization between the two blur the lines between who's who. A summer-flying *glaucus*-like swallowtail that may be a hybrid between *P. canadensis* and *P. glaucus* occurs throughout most of eastern Ontario. This situation was recently reviewed by Wang (TEA, Ontario Lepidoptera 2017). The purpose of this note is to provide further information on the distribution and identification of Ontario's tiger swallowtails, and to identify knowledge gaps that butterfly enthusiasts can help fill in. It is hoped that this will raise awareness of the fact that there are still considerable research needs among the most conspicuous of all Canadian butterflies. The database of the Ontario Butterfly Atlas (Macnaughton et al. 2018) was used to generate distribution maps, phenologies, and to re-examine species identifications.

The *Papilio glaucus* species group has a long history of changing species concepts – prior to 1991, only one species was recognized and the Canadian Tiger Swallowtail (*P. canadensis*) was thought to be a subspecies of the larger, more southerly *P. glaucus*. But mounting evidence from many aspects of developmental biology, biochemistry and morphology showed that *P. canadensis* was in fact a separate species (Hagen et al. 1991). Much of what we know about the evolution of the *Papilio glaucus* group stems from over three decades of research by Mark Scriber and collaborators. Surprises continue: recently, the discovery of a new species in the Appalachian Mountains, *Papilio appalachiensis*, has sparked further research into species boundaries within tiger swallowtails, particularly the nature and role of hybridization in speciation. Modern molecular methods have provided unprecedented insight into the evolution of tiger swallowtails; perhaps the most astounding recent development is that the Appalachian Tiger Swallowtail evolved from hybridization between *P. canadensis* and *P. glaucus* some 400,000 years ago (see Kunte et al. 2011 and references therein). The same research shows that *P. canadensis* and *P. glaucus* diverged from each other about 600,000 years ago – a much older split than initially thought, showing that superficial similarities can be deceiving. The ecology and evolution of the Appalachian Tiger may help shed light on the nature of the hybrid swallowtails in Ontario (discussed below as “Midsummer Tiger Swallowtails”).

### **Canadian Tiger Swallowtail - *Papilio canadensis***

This is Ontario's most widespread tiger swallowtail, and does not pose any identification challenges north of about 46°N latitude as it is the only northern tiger. The southern range limit appears to be a sharp transition or gap (tens of kilometers) to the territory of *P. glaucus*, as it is elsewhere in the Great Lakes Region (Scriber et al. 2002), but the transition from *canadensis* to *glaucus* has not been studied or even well defined in Ontario. In Wisconsin, this zone is about 60 km wide and is marked by a rapid change in genetic makeup from *canadensis* to *glaucus* (Scriber et al. 2002). Despite the term “hybrid zone”, naturally occurring hybrid specimens are very rare,

likely owing to the drastic developmental differences between the two species and the high selective pressure this imposes against hybrids (Deering & Scriber 2002). More work is needed to carefully document the swallowtails that occur across the zone of transition from *canadensis* to *glaucus* in southern Ontario.

There are few verifiable records of *P. canadensis* at the southern range edge (Fig. 2), most consisting of “sight” records. However, a recent increase in high quality photographic records through iNaturalist and eButterfly will better define the range edge of *canadensis*. Historically, *P. canadensis* did not occur as far south as Ajax (P. Hall, pers. obs.), and it is largely absent from the Greater Toronto Area; a few recent records exist from the Markham – Oshawa region (e.g., iNaturalist), with records increasing eastward along the Lake Ontario shoreline, and to the north in the Oak Ridges Moraine. West of the GTA, *P. canadensis* extends south at least to southern Grey Co and Bruce Co, just south of the base of Bruce Peninsula (Fig. 1). There are isolated records from the vicinity of Goderich (<https://www.inaturalist.org/observations/37942838>) and Lambton Shores (<https://www.inaturalist.org/observations/26814691>) that are considerably further south, which require further investigation to determine if these are truly *P. canadensis*. No verifiable historic records were found south of Bruce County (Fig. 1).

The factors limiting the southern extent of *P. canadensis* are not well understood, but may include summer mortality of pupae due to high temperatures (Scriber et al. 2002), as well as competitive exclusion by *P. glaucus*. With climatic warming, the range of *P. glaucus* has shifted northward in the eastern US (Ryan et al. 2018), and likely also in Ontario. There may be a concomitant northward shift of the southern limits of *P. canadensis*, but as there are few verifiable photo or voucher specimen records spanning the past three decades, there is currently no evidence for this.

### **Eastern Tiger Swallowtail - *Papilio glaucus***

True *Papilio glaucus* has two (or more) generations per year. The pupae resulting from the offspring of the spring brood do not enter diapause, and instead emerge in the same year (Scriber 1996). Since the offspring of the summer brood must reach the pupal stage before the end of the growing season (and the onset of winter), the Eastern Tiger Swallowtail is limited to more southerly climes. With climatic warming, the northern range edge appears to have shifted northward to the GTA, as it has elsewhere (Ryan et al. 2018). Historical season summaries (e.g. TEA, Ontario Lepidoptera 1999) make note of the fact that tiger swallowtails were observed only after mid to late June in the GTA (presumably Midsummer Tigers, see below), but May to early June records are now relatively common for the region, suggesting a northward range shift of *P. glaucus*. Nonetheless, Eastern Tigers here are at the cusp of survival at the northern range limits, and may persist only intermittently because a single cold year, late spring frost or early fall frost would result in local extinctions. *Papilio glaucus* is considerably more cold-sensitive than *P. canadensis*, lacking the cryoprotectants (“anti-freeze”) present in *canadensis* (Kukal et al. 1991). Since the minimum climatic requirements for *P. glaucus* have been studied extensively

and precisely defined, it is possible to predict the maximum geographic extent based on accumulated thermal units (degree-days), similar to plant hardiness zones. In Ontario, the northern-most limits that *P. glaucus* could survive (Fig. 2) essentially corresponds to the limit of the Carolinian zone. Since swallowtails are good dispersers and are long-lived, individual *P. glaucus* adults undoubtedly disperse beyond this critical thermal limit, but any eggs and larvae beyond this zone would fail to complete development before the end of the growing season and perish.

### **Midsummer Tiger Swallowtails**

What happens north of the range limits of true *P. glaucus* is not entirely clear. Although eastern Ontario is well north of the hybrid or contact zone between *P. glaucus* and *P. canadensis*, a late-flying swallowtail occurs throughout the region. In the literature, this swallowtail has variously been called *P. glaucus* (Layberry et al. 1998; Hall et al. 2014) “false second generation” (Hagen and Lederhouse 1985), “late flight *P. canadensis*” (Scriber and Ording 2005), and hybrid *glaucus* x *canadensis* (Scriber 1992). It flies after the spring (and only) flight of *P. canadensis*, and it is not the second brood of any spring-flying swallowtails, instead being a single-brooded entity unto itself (Hagen and Lederhouse 1985; Scriber and Ording 2005). These Midsummer Tiger Swallowtails (MTS) express a mosaic of characters from both *P. glaucus* and *P. canadensis*, suggesting they are hybrids, yet they also differ from lab-produced hybrids in several significant ways, most notably their very delayed pupal emergence resulting in a single summer flight whereas lab hybrids emerge in the spring (Ording et al 2010). Following winter diapause, MTS pupae delay emergence for about 1.5 months, depending on temperature: applying the temperature and emergence times previously documented from northeastern US populations (Ording et al. 2010), the predicted emergence in eastern Ontario would be late June, precisely when the first MTS start appearing. The true taxonomic identity of the MTS remains an open question, but there is a possibility that it is a valid species resulting from hybridization events in the distant past, similar to the evolutionary events that formed *P. appalachiensis* (Scriber & Ording 2005).

The earliest historical records of Midsummer Tiger Swallowtails are from the Frontenac Arch area of eastern Ontario in the 1970s; they were also documented in central New York in the 1980s. In the late 1990s, MTS started occurring in the Battenkill valley of Vermont (Scriber & Ording 2005), where they were previously absent. Scriber and Ording (2005) suggest that this reflects novel hybridization between *glaucus* and *canadensis* due to climate change, but it could equally well be range expansion of a previously more geographically limited taxon. The MTS has also expanded into the Ottawa area in the last two decades; it was unknown from the region in the 1980s, but is now widespread (Fig. 3) and frequent. The southern limits of MTS are unclear; preliminary molecular results establish MTS at least as far south as the Niagara region (Fig. 3). It is possible that the MTS has been present in southern ON for a very long time. Saunders (1874) provides this tantalizing bit of evidence from the London region over a century ago:

“[The tiger swallowtail] appears first on the wing from the middle to the latter end of May, but becomes much more plentiful in July. Whether these July insects are a second brood, or whether the bulk of the chrysalids which have wintered do not mature until about this time we are unable to determine.”

Saunders’ statement seems to suggest the presence of two taxa, a spring (*glaucus*) and summer (MTS) swallowtail.

### Identifying Tiger Swallowtails

Distinction of *glaucus* vs. *canadensis* is an issue in a relatively small geographic area, i.e., where the ranges of the two species approach each other (Figs. 1 and 2). The spring flight of *glaucus* and *canadensis* overlap, but specimens from early July onward are unlikely to be *canadensis* in this region. The morphological distinctions between the two are summarized in Table 1. Bryan Pfeiffer’s blog also nicely summarizes and illustrates the differences between the two (<https://bryanpfeiffer.com/taming-the-tigers/>). It’s important to note that spring *glaucus* can sometimes be *canadensis*-like, as discussed by Pavulaan & Wright (2002). This means that spring *glaucus* can have a banded or nearly banded forewing submarginal band, and a wider-than-usual black hindwing anal margin, in addition to being smaller like *canadensis*. Although many of the diagnostic characters can vary for spring *glaucus*, it is unlikely that all these traits would be *canadensis*-like simultaneously; more study is needed on the morphological variation of both species near the contact zone, and especially spring specimens from within the *glaucus* range.

North of the range of *P. glaucus* (roughly north of the GTA), the identification challenge is separating Canadian and Midsummer Tigers. A combination of date and location will usually separate the two: the peak flight time of *canadensis* is from late May to about June 10<sup>th</sup> in eastern Ontario. Late stragglers after June 20<sup>th</sup> are rare, and are essentially limited to the cooler regions such as the Algonquin dome and adjacent uplands (Lanark highlands, Haliburton highlands, etc). The Bruce Peninsula also has a higher frequency of late *canadensis* records, some of which have erroneously been attributed to *P. glaucus* or MTS, and these late records are probably the result of cooler climatic lake effects. In the region of range overlap between *canadensis* and MTS, specimens from mid June to mid July should be evaluated in terms of flight wear, location and morphological traits. External differences between *P. canadensis* and MTS are given in Table 1 and Figures 4-6. The most reliable traits are the width of the black anal margin (measured at the Cu2 vein junction as illustrated by the red line in Figure 5); this black band is proportionally wider in *canadensis*, although there is some overlap; the wider margin also results in the large black “V” appearing more sharply angled, versus more U-shaped in MTS. The amount of orange scaling capping the iridescent blue spots is also more extensive in *canadensis*. A clear view of the male clasper usually shows more interspersed black scales in *canadensis*, whereas MTS has a solid yellow clasper (Fig. 6). These traits can often be evaluated in photos, but a clear underside view is necessary.

Currently the most challenging identification problem is the separation of *P. glaucus* from MTS. Within the range of *P. glaucus*, the current thinking is that spring (before mid-June) specimens are *glaucus*, whereas MTS does not start flying until mid- to late June. The reliability of differential diagnostic traits between the two remains to be worked out, although trends in morphological differences are certainly evident.

**Table 1.** Comparison between three tiger swallowtail taxa.

<b>Trait</b>	<b>Canadian ST</b>	<b>Eastern ST</b>	<b>Midsummer ST</b>
1. yellow submarginal band - ventral forewing (Fig. 4)	Solid band, or coalesced squarely rounded crescents	Separated to coalesced rounded crescents	Separated to coalesced rounded crescents
2. width of black anal margin band - ventral hindwing (Fig. 5)	50-90%	10-40%	30-55%
3. relative size	small	large	Intermediate-large
4. male clasper scales (Fig. 6)	with sparse black scales	Solid yellow	Solid yellow
5. abdomen lateral black line	wide	intermediate-narrow	narrow
6. peak flight period	May-June	May-June; August	early to mid July

### **Comments by region**

The eastern shoreline of Lake Huron is in a transition zone from *canadensis* to *glaucus*. For Huron County, there are only a few records for May and early June (none of which are verifiable), and they are all from the early 1980s or earlier. The flight phenology (Fig. 7) shows a peak in early to mid July (likely Midsummer Tigers) and very few other records. Given the location it is likely that the few historical spring records may have been *P. canadensis*, which is near the southern range limit here. There is no evidence for true *glaucus* this far north, and it is beyond the thermal limits predicted by the developmental physiology of the species although dispersing individuals are possible. The bulk of the records are probably MTS. South of Huron Co., in Lambton Co., there is a marked change in phenology pattern with an extended flight of

tigers from late May into August (Fig. 7). This is consistent with the presence of true *glaucus* flying in the spring and again in the late summer, with a flight of MTS interpolated between the *glaucus* flights, but the presence of both taxa here requires confirmation. In the Hamilton-Waterloo region, the pattern is slightly different, and the lull between the spring and summer flights seen further south appears to be absent. A possible explanation for this is that MTS is sympatric and confounded with *P. glaucus* here, resulting in an essentially consistent emergence of swallowtails throughout the spring and summer. However, it is not yet clear why there is no pronounced August flight peak that corresponds to the second brood of *P. glaucus*, as there is in southernmost Ontario (Essex Co.). In Essex Co (Point Pelee and surrounding regions) *P. glaucus* is dominant, but it is not known if MTS also occurs there, as the slight peak in mid June seems to suggest. Alternatively, there may be two ‘flushes’ or peaks of spring-emerging *glaucus*, with a pronounced second-brood flight in August. A similar phenology pattern occurs in Norfolk Co further north along Lake Erie.

In summary, considerable gaps in our knowledge of Canada’s showiest butterflies remain. How far south does *P. canadensis* occur, and does it overlap at all with *P. glaucus*? What is the relationship of the Midsummer Tiger Swallowtail to these two? Despite the pronounced ecological differences, do *P. glaucus* and Midsummer Tigers appear differently where they overlap, or do they blend together? To what extent are the ranges of tiger swallowtails shifting in response to climate change?

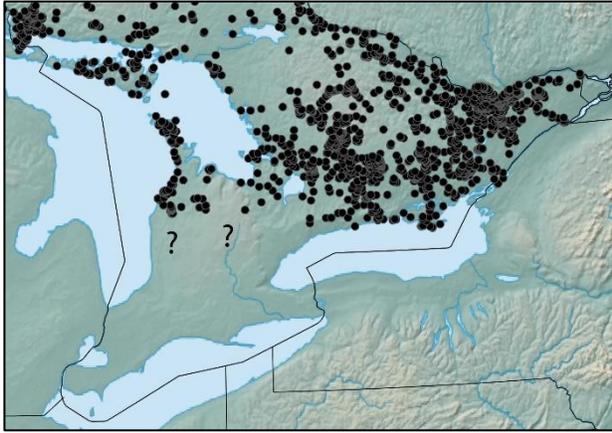
### **Acknowledgements**

I thank Rick Cvasin, Peter Hall and Xi Wang for critical comments on earlier drafts of this note, and insightful discussions on Ontario swallowtails.

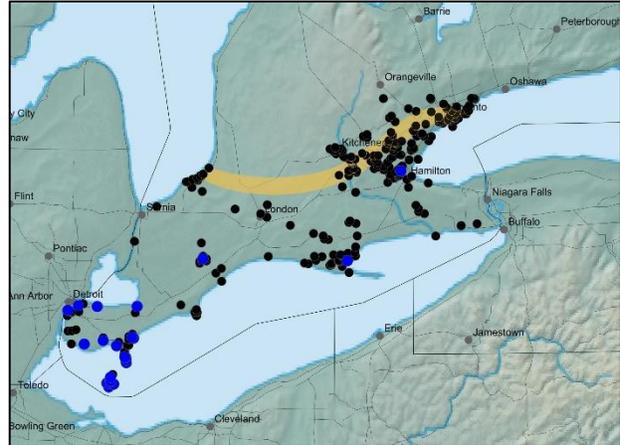
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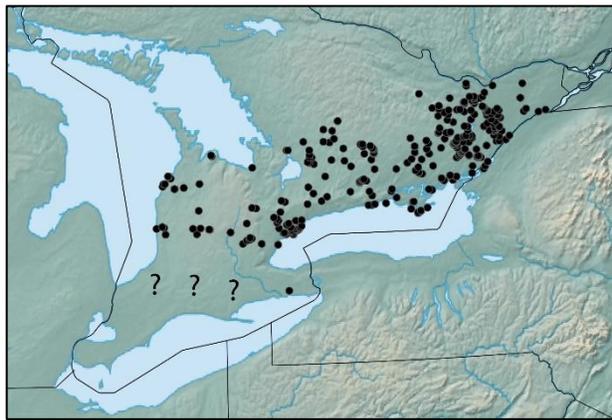
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**Figure 1.** Distribution of *Papilio canadensis* in Ontario, based on Ontario Butterfly Atlas records up to 2017. Records are filtered to exclude those that are possibly attributable to non-canadensis by: 1) excluding all records later than June 14th south of 46°N latitude (to exclude potential Midsummer Tiger records), and 2) excluding unverifiable records that do not have associated specimens or adequate photos, along the southern range limit to exclude potential *P. glaucus*.



**Figure 2.** Distribution of *P. glaucus* in Ontario, based on filtered Ontario Butterfly Atlas records. Blue circles indicate records of the dark female form which is unique to *P. glaucus*. Black circles are records only prior to June 1st, to exclude possible Midsummer Tiger Swallowtails. Shaded line indicates the northern thermal limit for *P. glaucus* (modified from Ryan et al. 2018).



**Figure 3.** Distribution of the “Midsummer Tiger Swallowtail” in Ontario. Records are filtered to exclude those earlier than July 1st for the region south of the Canadian Shield uplands to exclude potential *P. canadensis*. Also excluded are July records from within the range of *P. glaucus* (Fig. 2), since it is not currently known if the two can be reliably separated. The Niagara record is based on identification verified through molecular markers.



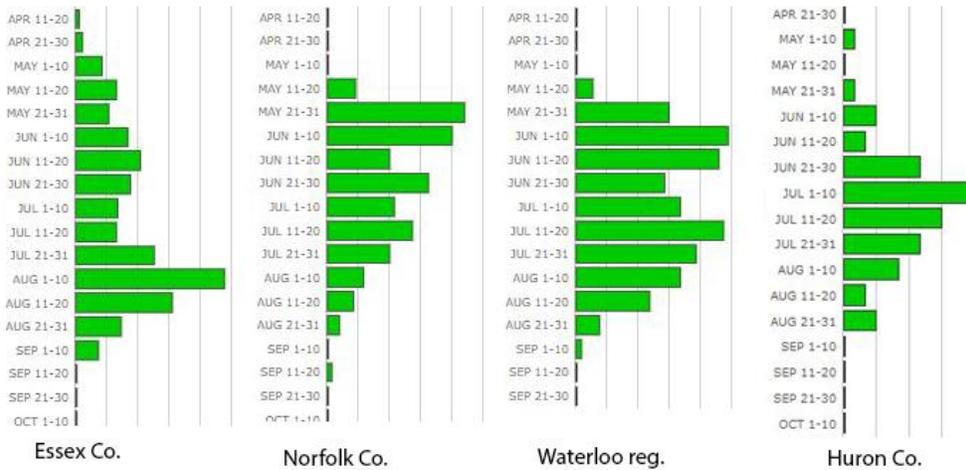
**Figure 4.** Forewing underside: comparison of the yellow subterminal band of the forewing in Canadian (top row) and Midsummer Tiger Swallowtail (bottom row). Note the greater tendency for a solid band and more squared-off shape of coalescing yellow spots in Canadian Tiger Swallowtail.



**Figure 5.** Hindwing underside: comparison of the anal margin black band of Canadian (left column) and Midsummer Tiger Swallowtail (right column). Note wider black band as measured at the junction of vein Cu2 (red line in top left image), narrower and sharper black “V”, and more extensive orange scaling in Canadian Tiger Swallowtail.



**Figure 6.** Male claspers: Canadian Tiger Swallowtail (top row), showing more interspersed black scales compared to the solid yellow scaling of the Midsummer Tiger Swallowtail (bottom row).



**Figure 7.** Comparison of swallowtail observation dates from four regions of southern Ontario (source: Macnaughton et al. 2018).