Tiger Tales: Natural History of Native North American Swallowtails

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The first drawing of a North American butterfly was of a male tiger swallowtail, produced more than 400 years ago by John White in an area now called North Carolina. White was the commander of Sir Walter Raleigh’s third expedition to the North American continent to an area generally referred to as Virginia. The stylized watercolor drawing was done by White in 1587, apparently after a Native American Indian boy presented him the specimen of this “manangwas” (“butterfly”), and was later reproduced as a wood-cut in the very rare book Insectorium sive Minimorum Animalium Theatrum (Holland 1931, Tyler et al. 1994).

Even today, as one of the most notable North American natives, the tiger swallowtail butterfly is abundant and widespread. From the male specimen, Linnaeus named the tiger swallowtail Papilio turnus, which he assumed to be a different species than the dimorphic dark female morph called Papilio glaucus L. It is now known that P. glaucus, which has both dark and yellow form females, occurs throughout the eastern half of the United States. Other smaller taxa were described north of the Great Lakes as P. g. canadensis Rothschild & Jordan and in Alaska as P. g. arcticus Skene. Both of these smaller species (currently =canadensis) lack the dimorphic dark form female. In the south, a putative Florida and Gulf states subspecies, P. g. australis Maynard, and the Mexican swallowtail species, P. aleixares Hopper, have been described, both with dimorphic (dark and yellow) females. Three largely sympatric species of tiger swallowtails occur in the western half of the United States (P. rutulus Lucas, P. eurymedon Lucas, and P. multicaudatus Kirby). All three apparently lack the dark morph form of females and have been variously reported to have local varieties, subspecies, and aberrations of form.

Our research group has been investigating the comprehensive natural history, ecology, and evolution of the North American swallowtails. We have conducted field and laboratory experiments to determine the host use abilities for Salicaceae, Betulaceae, Platanaceae, or Rhamnaceae (derived at E). Limited information is currently available on P. pilumnus and Central American and South American P. garamas and P. scamander; however, we have analyzed their hybrids with the P. glaucus and P. palamedes group. Total number of families is approximately 1,000, and total number of their offspring bioassayed is in excess of 25,000 individual larvae. Recent placement of the South American scamander and Central American garamas closer to glaucus than troilus may suggest that the ability to detoxify certain Magnoliaceae may have had a single origin instead of multiple origins in different continents (see Table 1).
and systematics of these North American *P. glaucus* and *P. troilus* swallowtail butterfly species groups and their closest Central and South American relatives for 15–20 years. The compulsion to study this tiger swallowtail complex and their sister group (the *P. troilus* complex) was catalyzed by an undergraduate writing assignment in 1969, which required a geographical and ecological analysis of the distributions and abundances of the species in the two complexes with a discussion of the biotic and abiotic factors (historic and current) that appeared to limit the range of species involved. This article describes recent progress toward completion of that project with continued experimental investigation of causes that delineate the range of this primitive, polyphagous, and indigenously North American *glaucus* complex in comparison to the related sister *P. troilus* complex.

**Basic Natural History of Life Stages**

Unlike most of their more tropical relatives (approximately 500 species), the tiger swallowtails of the temperate/boreal forests of northern North America spend from four to eight months as diapausing pupae, often under snow. This is possible because of physiological adaptations that enhance acclimation and survival under very cold temperatures (possibly because of the presence of ethylene glycol or related cryoprotectants [Kukal et al. 1991]). The escape of tiger swallowtails from the specialization on tropical host plant families (e.g., Rutaceae, Lauraceae, and Magnoliaceae) that, with the Aristolochiaceae, Apiales, and Annonaceae, comprise the diets of 90–95% of all swallowtail butterfly species, and their persistence at high latitudes, has made them doubly unique among the world’s Papilionidae.

In the spring, adult males eclose, begin to fly, and search for emerging females with which to mate. These males may fly along canyons of the Rocky Mountains, streams of the boreal forests across Canada, or hedgerows and islands of trees from Florida to Maine and northward. They may live 1–2 months and may mate several times. We have observed with spermatophore counts that females also mate several times (up to five or six) during the course of their 3–6 week natural life span in the field. A series of compressed spermatophores can easily be counted upon dissection of multiply-mated female abdomens. We have shown that multiple matings are important for restoring female fertility, which usually declines rapidly after about one week of oviposition (i.e., 7–8 days postmating). A successful mating consists of the transfer of the male spermatophore, which can be of variable size, into the female’s bursa copulatrix. It is believed that sperm from the most recent spermatophore fertilize the eggs laid subsequently (i.e., sperm precedence).

Eggs are fertilized as they are oviposited singly onto host plant leaves. The *P. glaucus* group generally prefers to oviposit on the top of leaves and the three Lauraceae-specialized members of the *P. troilus* group (*P. troilus* L., *P. palamedes* Drury, and *P. pilumnus* Boisduval) on leaf bottoms. Eggs develop and change to a yellowish or darker brown color before eclosion of the neonate larva. Eggs in the *P. glaucus* group are initially green, whereas eggs in the *troilus* group species are yellowish. Normal-colored *P. glaucus* adults, which have been reared as larvae on artificial diet, produce eggs that are basically blue or turquoise. The eggs are much the same color as the blue larvae that result when *P. glaucus* are fed diets that lack carotenoids found in normal host plant leaves.

Egg development to larval eclosion is thermally sensitive and generally requires 5–10 days under normal field conditions. The first instar often eats the egg shell and proceeds to lay down a silk mat on the leaf surface, thus providing a firm attachment. This behavior results in a leaf roll in which the larva hides. However, *P. glaucus* larvae generally are exposed and do not form complete rolls of the leaves they rest upon.

Larvae of tree-feeding swallowtails spend most of their time resting on leaves of their host plant, but may change location several times throughout their 3–5 week lives. For *P. glaucus*, neonate and second instars usually feed at the edge of the leaf where their mother placed the egg. Location changes usually occur immediately premolt or postmolt. With patience, one can observe feeding bouts of 1–2 minutes, which are spaced several hours apart in mid- to late instars. In contrast, movement to a new leaf for feeding, with a return to the same resting pad, is common for third to fifth instars. The distance traveled from resting to feeding site can be several feet, and it is common for mid-late instars of *P. glaucus* (and probably other species of the group) to gnaw through the petioles of the leaves they have just fed on until the partially consumed leaves fall to the ground. This leaf-
The P. glaucus Species Group
gnawing or leaf-clipping behavior may remove evidence of caterpillar presence to natural enemies that locate hosts by olfaction (e.g., hymenopteran parasites) or, perhaps, those that use leaf feeding damage as a visual clue (possibly birds as well as human researchers). It is also feasible that this behavior prevents chemical induction in leaves that are adjacent to damaged leaves and now may be of lower quality or are toxic for subsequent larval feeding. Although allelochemical induction has been a hot topic for the past two decades, it is not known what selection pressure may have shaped the leaf-clipping behavior in *P. glaucus* nor how extensive it is on various host plant species. Perhaps swallowtail larvae do not clip leaves on plants that do not express chemical induction.

Whereas larval growth rates of all insects are temperature-determined to some extent, our group has learned that nutritional quality, or suitability, of host leaves is the major determinant of larval development rates. However, temperature is also significant in the development of life history traits (i.e., strategies) and interacts with leaf quality at different latitudes. For example, seasonal constraints determining the number of generations per year, and the need for reproductive synchrony of these populations, have resulted in basically predictable annual flight periods at such locations. The first flight of *P. glaucus* in the United States is usually in early March when new southern Florida butterflies appear. The first flight of *Papilio* elsewhere occurs as spring moves northward across the continent. By late May, *P. glaucus* and *P. canadensis* may be simultaneously on the wing from the central United States all the way to Alaska. A second generation of tiger swallowtails is usually observed from the Great Lakes southward to the Gulf States from Texas to Florida, where a third or even fourth flight may occur.

Altitudinal variation in seasonality and volitism is also important. Should the wrong host choice be made by ovipositing *P. glaucus* or *P. canadensis* females at certain locations (e.g., at high elevations or high latitudes), larvae may not successfully complete development to the pupal (overwintering) stage. From the Great Lakes region northward to Alaska, only a single generation is possible, even on the best host plants (Ayres & Scriber 1994). The northernmost populations are photoperiodically insensitive obligate diapausers. Cold pockets, or phenological depressions, are known locally in sections of northern Michigan and Wisconsin, where conditions are more similar to central Alaska than to geographic regions elsewhere in the continental United States (Scriber 1994). Butterflies in the thermal depressions of Michigan also have short growing seasons and experience more severe seasonal constraints than those in surrounding counties. Although there is a gradual latitudinal decline in forewing length from Florida (62–66 mm) to Alaska (42–44 mm), there are exceptions where locally smaller adult sizes are found in cold pockets of Michigan (40–43 mm) than otherwise observed in other populations at similar latitudes (45–50 mm) (see Scriber 1994). At the same growth rate, a *Papilio* caterpillar that pupates at a smaller size will complete its growth before another that continues to grow to a larger size. Such early pupation behavior for smaller caterpillars may allow survival that would otherwise be impossible in such thermal depressions. Although many other natural selection pressures and ecological variables may affect adult size, such size reductions greatly enhance the odds for rapid pupation and thus seem exceedingly important by assuring that they may reach this diapause stage before winter sets in.

The combination of cold tolerance and generalized feeding abilities on nontropical host plant families (e.g., Rosaceae, Oleaceae, Salicaceae, Betulaceae, Tiliaceae, Platanaceae, and Rhamnaceae) have doubtlessly been major factors permitting the radiation of six species of the *P. glaucus* group of swallowtail butterflies into the higher global latitudes. Both adaptive suites of traits (winter survival and polyphagy) are considered rare in swallowtails and both may be a partial explanation for the decline in species richness of the Papilionidae from tropical to boreal habitats.

**Molecular and Biochemical Phylogenetics of the Group**

The phylogenetic distinctions suggested in 1959 by Lincoln Brower (based on various morphological, color, and genital traits for the eight North American species of Munroe's section III of the Papilionidae [1961]), basically agrees with our analysis of 26 electrophoretic allozyme loci for these same species. Our laboratory has found sufficient differentiation among *P. glaucus*, *P. rutulus*, *P. erymedon*, *P. multicaudatus*, and *P. alexiarae* for each to be considered a distinct species, confirming earlier suggestions by Brower and Munroe. We have recently (Hagen et al. 1991) added *P. canadensis*, which was previously...
regarded as a subspecies or seasonal variant of *P. glaucus* for 200 years. There was no evidence of differentiation between the Florida subspecies *P. glaucus australis* Maynard and *P. g. glaucus* from other regions. There was also insufficient allozyme differentiation to distinguish *P. canadensis* from the putative Alaskan subspecies *P. canadensis arcticus*. Also we recognized three distinct species in the *P. troilus* group in section III: two subspecies of *P. troilus* L. (*P. t. troilus* on the coast and *P. t. ilioneus* inland), *P. palamedes* Drury, and *P. pilumnus* Boisduval. All of these are more closely related to each other than to any of the six *P. glaucus* species.

Within the *glaucus* group, the most surprising phylogenetic relationships were that *P. glaucus* and *P. canadensis* are different species and that the Mexican *P. alexiarias* appears more closely related to *P. glaucus*.
(left) Assorted mortality causes and natural enemies of *Papilio* in North America. (A) Leaf-cutter ants, *Atta texana* (Buckley) carrying off pieces of sassafras leaf, some of which had *P. troilus* eggs, in the Big Thicket of East Texas. (B) Forest tent caterpillar, *Malacosoma disstria* Hübner, at the edge of severe defoliation beginning consumption of a small choke cherry seedling with a *P. canadensis* egg (green, lower right) in northern Wisconsin. (C) Tachinid fly pupae from *P. glaucus* fifth instar larva. (D) Mite eating neonate (first instar) *P. troilus* on sassafras tree in Ingham County, Michigan. (E) Parasitoid (*Trogus* sp.) searching for additional larvae immediately after stinging fifth instar *P. glaucus* on tulip tree in Ingham County, Michigan. (F) Common scene for both *P. glaucus* and *P. canadensis* (here) is this pentatomid (*Podisus* sp.) feeding on hemolymph from impaled larva. (G) *Formica* sp. ants killing *P. canadensis* larva on black cherry in northern Michigan.
than is *P. canadensis*. Secondly, the sympatric western species *P. rutulus* and *P. eurymedon* were found to be sister species with extremely little divergence in biochemically detected genetic traits. Sperling's (1993) restriction site analysis of mitochondrial DNA produced phylogenies that were basically concordant with the allozyme phylogenies for the *glaucus, canadensis*, and *alexiares* relationships, and the *rutulus* and *eurymedon* relationship.

Although virtually identical in mtDNA and allozymes, *rutulus* and *eurymedon* clearly are different species. They express different adult wing color patterns, larval host use traits, and oviposition preferences, in addition to different wing morphology, genitalia, and mating preferences (Brower 1959). However, we have found (Hagen & Scriber 1995) that hybrids between these two species are unusual for *Papilio* hybrids because they do not show the Haldane effect (sterility or deficiency of the heterogametic sex among offspring in *F*₁ hybrids; in birds and Lepidoptera, it is generally believed that females are XY, or heterogametic, and males are XX, or homogametic). The lack of Haldane effect implies a close genetic relationship between *rutulus* and *eurymedon* and a lack of major adaptive differences controlled by factors on the sex chromosomes. This contrasts with the *P. glaucus* and *P. canadensis* sister taxa, which differ quite significantly for traits on the sex chromosomes (e.g., diapause regulation, adult wing polymorphism, suppressors of dark morph female color, and differential oviposition preferences for certain species of the Salicaceae and the Magnoliaceae host plants as well as Haldane effect; Scriber 1994). There is doubtlessly a fascinating role involving various sex-linked factors, including the Haldane effect, in speciation processes of these butterflies that needs to be clarified.

**Host Plants and Range Limitations for Tree-feeding Swallowtails: Evolution of Polyphagy in Papilionidae**

Of the 560 or more species of Papilionidae in the world, about 65% feed on one of five tropical plant families (Rutaceae, Apiaceae, Aristolochiaceae, Anonaceae, or Lauraceae). The two most polyphagous species are the North American *P. glaucus* and the South American *P. scamander* Boisduval. Both species feed on dozens of host species from five to nine plant families. Traditionally, these butterflies have been taxonomically considered representatives of different sister sections (III and V) (see Table 1) of the family. In contrast to conventional wisdom of the past 4–5 decades, our interspecific hybridization studies between *P. glaucus* and *P. scamander*, and pairings of each with the Lauraceae-specialized North American *P. troilus* and *P. palamedes*, suggest a closer genetic relationship between the *glaucus* and *scamander* groups (both extremely polyphagous) than between the *glaucus* and *troilus* groups (both North America). Based on mtDNA analyses, Sperling (1991) added evidence that the polyphagous *P. scamander* and its relative in Central America, *P. garamas* Hubner (or *P. abderus* Hopffer) of the *P. homerus* group, may be more closely related to the North American *P. glaucus* group than are the North American Lauraceae-specialized *P. troilus* group.

These findings raise questions about whether a generalist ability to feed on the Magnoliaceae, the Lauraceae, and several additional plant families may have originated only once, in a common ancestor of the geographically widely separated *glaucus* and *scamander* species. With a probable phylogeny based on our findings, this and other questions may be more rigorously addressed. What are the specific detoxication mechanisms and biologically active phytochemicals...
involved with differential host use abilities? Are the toxic chemicals also the cues for adult oviposition avoidance? Have these behaviors and abilities evolved many times, independently, or only once? How do adult oviposition preferences correlate with larval detoxication capabilities on the hosts? With regard to physiological detoxication abilities or behavioral oviposition preferences, which are evolutionarily more stable or labile? What role do host plants and differential detoxication abilities play in the speciation process, and are close host affiliations the major explanations for the current geographic distribution of North American species of the *P. glaucus* group? What are the dynamics and causes of the narrow zone of overlap/tension/hybridization or genetic introgression between *P. glaucus* and *P. canadensis* that has been maintained for at least 100 years in the Great Lakes and Appalachian mountain plant ecotones? What are the key adaptive traits and environmental limitations that determine the thermal ecology, diapause physiology, genodynamics (local dispersal, introgressive hybridization, sex-linkage, genetic hitch-hiking, etc.), and current distributions of North American swallowtail butterflies?

Although *P. glaucus* larvae have the capability to develop on woody plants in at least 10 families, other species and subspecies within the *P. glaucus* group differ significantly in their ability to survive and grow, particularly on Magnoliaceae, Lauraceae, Rutaceae, Salicaceae, Betulaceae, Platanaceae, and Rhamnaceae. The *P. troilus* group species are phytochemical specialists with larvae feeding only on particular species of Lauraceae at a given location. The combination of phytochemical affiliations and glacial phytogeography have doubtlessly played major roles in determining the distributions of key host plants and butterfly species in these two species groups. For example, the Magnoliaceae and Lauraceae are primarily found in the southeastern part of North America, as are those affiliated butterfly species. *P. glaucus* is found on sweetbay or tulip tree of the Magnoliaceae.

Range of the model species, *Battus philenor*, and the geographic position (solid black band) of the average seasonal thermal unit accumulations corresponding to 1,390–1,500°C degree-days above a base threshold of 10°C. These data were assembled from various state publications and are based upon 20–30 year averages generally between 1950 and 1980 (see text for discussion).
Table 1. Species within the Papilionidae family (modified from Munroe 1961)

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<th>Section</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. species*</td>
<td>9</td>
<td>143</td>
<td>9</td>
<td>35</td>
<td>20</td>
</tr>
<tr>
<td>Primary host-plant families*</td>
<td>Lauraceae, Rutaceae, and less commonly on Apiaceae (=Umbelliferae)</td>
<td><em>glaucus</em> complex on Magnoliaceae, Lauraceae Rutaceae, Rosaceae Salicaceae, Betulaceae, Oleaceae, Platanaceae, Rhamnaceae</td>
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<td><em>macbaon</em> group also on Compositae</td>
<td><em>scamander</em> group, and <em>homerus</em> group on Lauraceae, Hernandiaceae, Magnoliaceae, others</td>
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<td><em>troilus</em> complex on Lauraceae</td>
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Geographic ranges were as follows: Section I, Africa, Asia, and IndoAustralia; Section III, worldwide; Section II, North America; Section IV, Central America; Section V, Central or South America.

* Includes the six *P. glaucus* group species (*glaucus, rutulus, eurymedon, multicaudatus, alexiaraes, and the recently added canadensis; see fig. 2).
* *Scamander* group species consists of *P. bellanichus* Hewitson, *scamander* Boisduval *birchalli* Hewitson, and *xanthopleura* Godman and Salvin.
* *Troilus* group consists of *P. troilus*, *P. palamedes*, and *P. pilumnus* (see fig. 3).

and *P. palamedes* on redbay of the Lauraceae (whereas *troilus* feeds on redbay in Florida, it prefers spicebush or sassafrass elsewhere). Similarly, the western and northern distribution of key Salicaceae and Betulaceae species across North America basically corresponds with that of *P. canadensis* or *P. rutulus* (see Scriber et al. 1991). Because these polyphagous *glaucus* group species transcend the range of any single host species, other biotic and abiotic factors must contribute to geographic range limits (and the dynamics of gene flow).

Although genetically based interspecific and intraspecific differences in host plant acceptance, detoxication, and larval growth abilities exist among North American swallowtails, we have observed a wide range of reported and potential plants (more than 70 species from 12 families) that are capable of supporting successful development. Sufficient phenotypic and genotypic variation in ovipositional behavior has been observed in all *P. glaucus* group species tested, thus allowing ecological mistakes and possibilities for evolutionary host shifts. Although heritable and behaviorally fixed preferences for natural hosts are generally observed in multichoice laboratory studies, an average of 2–8% of the plants selected for oviposition in these studies are nonhosts or toxic for larvae (Scriber 1993). Although some of the patterns of ovipositional preference have been shown (via reciprocal, hand-paired hybrids) to be sex-linked in *P. glaucus* and *P. canadensis* (for quaking aspen or tulip tree [Scriber 1994]), the differential detoxication abilities in larvae appear to be based on autosomal traits. Recent work with *P. glaucus* (Bossart & Scriber 1995) suggests that in some cases, there is a correlation of adult oviposition preference and larval growth performance. However, this may be the exception rather than the rule for phytophagous insects.

Our studies of neonate larval survival on, and adult ovipositional behavior toward, various potential hosts suggest some rather stable phylogenetic constraints on host range in certain Papilio. However, the variation that is present is sufficient to permit natural selection to effect some major host shifts. Based on these contrasting observations, we conclude that the role of past and current host plant distributions in determining geographic range limits for these native North American butterflies is preeminent but not exclusive (see Fig. 1; Suggested Readings)
Biotic Factors that Affect the Geographic Range Limits of Species

In addition to host plant distribution, other biotic factors such as competing gene pools (i.e., inter- and intraspecific competition), parasites, and predators may play major roles in determining whether a particular swallowtail butterfly is absent or rare in a particular area of North America. For example, extensive gypsy moth defoliations (750,000–1 million acres annually) have imposed a serious impact on two *Papilio* species in Michigan. Furthermore, there are associated natural enemies that increase with gypsy moth populations (e.g., the parasitic and polyphagous tachinid fly *Compsilura concinnata* Meigen), that also cause serious mortality in some populations of *P. canadensis* and *P. glaucus* at distances more than 50 miles ahead of the gypsy moth defoliation front. More important to the local population dynamics of native swallowtails is the effect of extensive aerial application of pesticides for gypsy moth control. We have observed that the microbial pesticide from *Bacillus thuringiensis kurstaki* Berliner can kill *Papilio* species for 20, 30, and 40 days after spraying on tree leaves sprayed at 16 BIU (billion international units)/acre aerial application rates used for gypsy moths. Such interactions of microbial pesticides with nontarget arthropods (including natural enemies) warrant considerable research because the available information is so sketchy at this time. Diseases also may be devastating in some geographic or topographic areas depending on habitat, microclimate, and even the species of host plant that larvae feed on. The role of various generalist and specialist natural enemies (see Fig. 4) in *Papilio* population dynamics is currently under investigation. We hope to determine the relative importance of these native and introduced agents in the evolution of diet breadth in *Papilio* relative to other causes such as competition, chemical coevolutionary constraints, and the voltinism/suitability hypothesis (see Scriber & Lederhouse 1992).

Perhaps the most familiar example of the potential significance of natural enemies on the distribution of *P. glaucus* is related to the adult dark morph (mimetic) color polymorphism found in some portion of *P. glaucus* te-
males from the Great Lakes into Mexico. For decades, it has been presumed that the dark morph females mimic the distasteful pipevine swallowtail butterfly, Battus philenor L., and that the frequency of dark form females is higher where the selective advantage is greater because of large populations of the model species. This argument is basically believable; however, the recent increased frequency of dark females in the southern half of Florida and the lack of any dark morphs in the southwestern United States, despite the occurrence of the model, imply the need for alternative explanations. Furthermore, the northern limits of the sex-linked (Y chromosome) dark morph gene seems to be more precisely delineated by abiotic factors (thermal unit accumulations of 1,400°C above a base 10°C developmental threshold) than by the geographic distribution of the distasteful model, B. philenor. A seasonal accumulation of degree-days fewer than 1,400 selects intensively against completion of a second generation for P. glaucus and other Lepidoptera (e.g., European corn borer) at this Great Lakes transition zone where a sex-linked obligate diapause regulation occurs. This sex-linkage of diapause regulation and dark color expression and suppression are described in more detail elsewhere (Scriber et al. 1995a).

The reason for the lack of complete fixation of the dark morph in females in areas of high B. philenor populations, such as the Smoky Mountains and Gulf states, has been suggested by various authors to result from a balanced polymorphism exerted by male mating preferences for yellow morph females. Robert Lederhouse has led our research group in evaluation of this hypothesis by observing male responses to tethered, size-matched females of different color morphs. Based on geographically diverse field studies over several years, we now conclude that male mating preferences will vary with the relative frequency of the two morphs at various locations and it seems doubtful that male intersexual selection could prevent the genetic fixation of the dark (mimetic) allele. For example, in Florida, where dark morph females have increased rapidly (from 5 to 35% of the population in 30 years), males are still much more likely to court and copulate with yellow morph females than with dark morph females. In southern Ohio, where dark morphs comprised 80% (or more) of the population, males were equally or less likely to copulate with yellow than dark morph females. The intensity of the selective advantage of this presumed mimicry remains unclear; however, we have observed that in the northern edge of the range, a sharp and predictable limit in the occurrence of mimetic dark morphs is basically independent of the model species. This dark morph range limit appears to result from several interrelated ecological factors (sex-linkage, voltinism, plant ecotones, hybrid zones, global warming, and Pleistocene glaciations).

Because host plant distributions are clearly related to temperature (extremes and seasonal degree-day accumulations), it is not surprising that plant ecotones (or transition zones) between life zones (e.g., Merriam's)
correlate with abiotic (thermal) factors. We have found that the center of the transition life zone of Merriam, which runs along Canada and across the Great Lakes region down into the Appalachian Mountains, is closely approximated by the seasonal thermal unit accumulation of 1,400 degree-days (above a base 10°C). Also, the center of this plant ecorezone (Fig. 6) is the precise northern limit of dark morph tiger swallowtail females, the northern limit of tulip tree detoxication abilities (which corresponds roughly to the northern range of tulip tree), and the northern limit of bivoltine (two generation) capabilities. The southern limits of aspen (Salicaceae) detoxication, suppression of the dark morph female, and presence of obligate (photoperiodically insensitive) diapause are known also to occur in this same narrow zone. We now know that this unique zone delineates the parapatric juncture of the Canadian swallowtail species, P. canadensis, and the tiger swallowtail. Limited hybridization at this zone is evident in subtle morphological intermediates and in genetic introgression detected using diagnostic allozymes. In the Great Lakes region, we see evidence of asymmetrical gene flow with southward introgression in Salicaceae detoxication abilities and X-linked color suppressor activity, but limited northward movement of Magnoliaceae detoxication abilities or of Y-linked dark morph genes. Additional research with allozymes and mitochondrial DNA may help clarify this picture.

**Sex Chromosomes and Hybrid Zone Dynamics**

Experimental investigations of various ecological determinants of range limits in P. glaucus have not only clarified the species status of P. canadensis, but have elucidated what may be a major evolutionary mechanism of speciation: sex-linkage of key life history traits (or coadapted gene complexes). With 30 sets of chromosomes, it seems especially provocative that we have located genes on the X-chromosomes of two *Papilio* species that control obligate versus facultative diapause, mimetic versus nonmimetic wing color, and differential oviposition preferences for aspen versus tulip trees. These genes have been mapped in relation to loci for five electrophoretic allozymes (Scriber 1994). The deleterious interspecific hybridization X-(Haldane) effect is also apparently controlled by loci somewhere on this chromosome, and it is likely that these losses in viability, fertility, or survival of heterogametic hybrids (females in Lepidoptera) would be a major selective force in hybrid zones where limited movement of sex chromosomes (compared to autosomes) has been observed for insects.

It is uncertain to what degree such accumulations of genes on the X-chromosome of *P. glaucus* and *P. canadensis* results from suppressed crossovers between the X and Y chromosomes or simply from faster rates of evolution of traits on the X-chromosome (e.g., recessive mutations) compared with those on the autosomes. In any case, this fascinating comparative autecological natural history and biogeographical survey of *Papilio* species groups has permitted a reductionist progression from field ecology into biochemical and molecular mechanisms that may help explain the genetic basis of adaptations for the various populations and species. These mechanisms, in turn, have helped to define the natural distribution limits of the taxa and to provide insight into the speciation process.

Our ability to hand-pair and obtain viable hybrids of almost every combination of species pairs among and between the North American *P. glaucus* and *P. troilus* groups (as well as with South American species) has facilitated our progress tremendously (Scriber et al. 1993b). It seems likely that only through a combination of approaches (e.g., descriptive and experimental, laboratory and field, molecular and ecological) will we be able to understand the temporal and spatial distributions and interactions of individuals, populations, and species. The phyto-chemical bases and genetic mechanisms of differential larval detoxication abilities have already been elucidated using hand-paired hybrids and backcrosses with bioassays on plants of the Salicaceae and Magnoliaceae families (Scriber et al. 1989). Although the geographic borders between *P. canadensis* and *P. glaucus* may be largely host-plant influenced and these separate rather distinctly at the plant transition between boreal and temperate forests (Hoffman & Blows 1994), we know little about intraspecific geographic differences in plant phytochemistry (Johnson & Scriber 1994) and even less about interspecific (or hybrid) phytochemistry and its influence on herbivores (Strauss 1994).

Life history traits cannot be studied effectively one at a time because of the interactive matrix of biotic and abiotic selective pressures that can simultaneously assault any particular phenotypic combination. The complexity of interactions among life history traits and the
dynamics of environmental forces may preclude any rigorous determination of the relative fitness of individuals with any given combination of adaptations because fitness must be evaluated in relation to the particular environment(s) encountered. Comparative studies of related species such as these Papilio groups, with differing degrees of genetic divergence and phylogenetic relatedness, provide a powerful approach to these and other fascinating but complex questions.

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