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THE

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TWO NEW ABERRANT FORMS OF TIGER SWALLOWTAIL BUTTERFLY FROM THE GREAT LAKES HYBRID/TRANSITION ZONE (LEPIDOPTERA: PAPILIONIDAE)

J. Mark Scriber[1]

ABSTRACT

Two aberrant forms of the tiger swallowtail butterfly. *Papilio glaucus*, are described. Both of these aberration types (one in a male, the other in females) are believed to be previously unreported and both are from the Great Lakes hybrid zone and plant transition zone ($41° - 44°$N latitude). It is, therefore, possible that genetic introgression from the northern tiger swallowtail *P. glaucus canadensis* may have been involved in some way with these abnormalities.

While the specific causes of aberrant forms of tiger swallowtail butterflies remain basically unknown, it has been noted that the frequency of unusual forms may be greater within, or near, the plant and insect transition zone (Curtis 1957, Remington 1968) that occurs throughout the Great Lakes region (Scriber et al. 1987). For example the distinctive *Papilio glaucus* "fletcheri" variety (Fletcher 1889), as far as reported thus far, occurs only in males and typically north of, or very close to the transition/hybrid zone of the *P. g. glaucus* L. and *P. g. canadensis* R. & J. subspecies (Scriber and Lintereur 1983; and T.J. Allen, D. Mutusik, H. Romack and J.D. Zelias, pers. comm.). A different "dark cell" aberration has a genetic basis and was reported only from females which also originated within the subspecies transition zone in Schuykill County, Pennsylvania (Scriber and Evans 1988a). A large series of 42 sexual mosaics and bilateral gynandromorphs of *Papilio glaucus* (most of which are from the hybrid zone) is illustrated and described by Scriber and Evans (1988b), and it is concluded that intersubspecific pairings may be conducive to the infrequent occurrence of bilateral gynandromorphs.

Another low frequency phenomenon that may occasionally be related to hybrid interactions between subspecies of *Papilio glaucus* is the occurrence of "melanic intermediates" in which the dark morphotype female has incomplete expression (see figures and descriptions in Clark 1932, Clark and Clark 1951, Scriber et al. 1987). In these "intermediate" females the underlying black tiger striping pattern may be clearly visible with mostly yellow background, appearing lightly "dusted," or they may be essentially non-distinguishable due to a much heavier suffusion of dark scales, resulting in an "intermediate" color series or continuum. While partial dark suppression from *P. g. canadensis* genes may be involved (Scriber et al. 1987, Scriber et al. in prep.), these "dark intermediates" are known from nearly every state east of the Mississippi River, and it has been shown that the phenomenon can be environ-

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mentally induced in *P. g. glaucus* by high temperatures (Ritland 1986, R.C. Lederhouse and J.M. Scriber unpublished).

A slightly aberrant "sooty" region basally in both the dorsal and ventral sides of the forewings and hindwings was noted in female *P. g. glaucus* by Clark (1932) and Clark and Clark (1951). A similar darkened inner wing pattern was subsequently noted in a male *P. g. glaucus* and certain of his unique offspring (possibly involving a chromosome abnormality) that included dark segregating females where they were not expected to be possible, including offspring of a *P. g. canadensis* female (Scriber and Evans 1986).

Here, two new and different types of aberrations are described, which have not been previously reported as far as is known. One of these aberrations was found in a male from the potential hybrid zone of *P. g. glaucus* and *P. g. canadensis*, and the other aberrant form is represented by two females of two different family lines from the same hybrid zone population in Green Lake County, Wisconsin.

RESULTS

In the last 8 years our lab has reared more than 40,000 tiger swallowtail butterfly larvae. We have reared approximately 20,000 to the adult stage. In addition, we have collected from widespread geographic areas across the eastern half of the country. Two types of aberrations are described below that we have not seen in any of the other individuals we have reared or collected in the field.

The first aberration, which is described in this paper, appeared in a male. In males, the blue scales in the submarginal area are usually reduced on the hindwings; however, this blue extends across most of the hindwings of females and often into the forewing. This aberrant male was reared from stock sent by William Houtz (Schuykill County, PA) and has the blue scaling essentially as in normal females (Fig. 1).

The second aberration occurred in two females reared from the same population in Green Lake County, Wisconsin. These females have an atypical melanism and atypical wing pattern (Figs. 2 and 3) compared to normal *P. g. glaucus* or *P. g. canadensis* (Fig. 2). The black band on the hindwing virtually fills the entire anal cell, and there is essentially no blue scaling on the dorsal or ventral wing surfaces as in most *P. g. glaucus* and *P. g. canadensis* females. These two females were reared from separate mothers, however, each originated from normal appearing yellow morph field-captured mothers from Green Lake County (see Table 1).

DISCUSSION

The control of blue scaling of the hindwings of *Papilio glaucus* subspecies has not been genetically determined yet (see West and Clarke 1988). There is also considerable variation in the blue scaling patterns observed among our voucher collection females (e.g. with blue scaling suffused across the entire dorsal surface of the hindwings) and males (with no blue scales). However, these two female individuals from Green Lake County Wisconsin represent an extreme case of reduced blue hindwing scaling and extra melanism. The aberrant male with unusually excessive blue scaling also represents an extreme case. It otherwise has basically similar patterns to other normal *P. g. glaucus* males. We know of no other previous record or existing specimens of these types.

We are unable to determine if introgression from hybrid interaction of *P. g. glaucus* and *P. g. canadensis* was involved in either of these aberrants (Figs. 2 and 3); however, both are from the near vicinity of the known subspecies hybrid zone across the Great Lakes region southward into the Appalachians (Luebke et al. 1988, Scriber and Hainze 1987). Other individuals caught in the exact location as the two females from Green Lake Co., Wisconsin do produce mixed color broods of daugh-
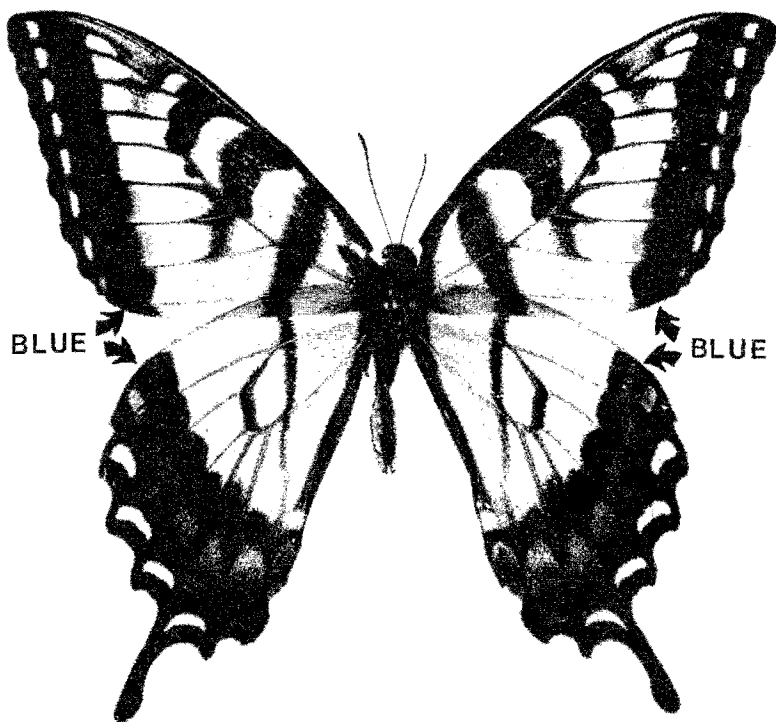
Figure 1.   Dorsal view of an aberrant male *P. glaucus* reared from a mother (#16) collected by W. Houtz from Schuykill County, Pennsylvania.

ters (both dark mimetic and yellow) and are often computer-scored as hybrids using multivariate discriminant analyses of male wing characteristics (Luebke et al. 1988), suggesting that subspecies introgression does occur in this area (Scriber 1990, and Scriber et al. 1990).

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Figure 2.   Dorsal view of an aberrant yellow female *P. glaucus* reared from the female parent (#1310) collected in Green Lakes County Wisconsin by J. Thorne, S. Sippl, and M. Evans.
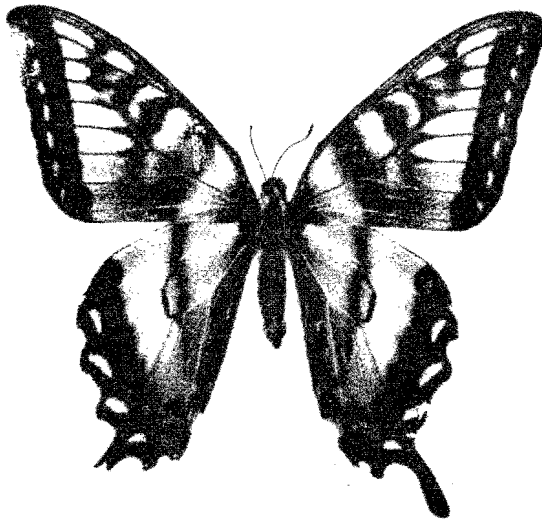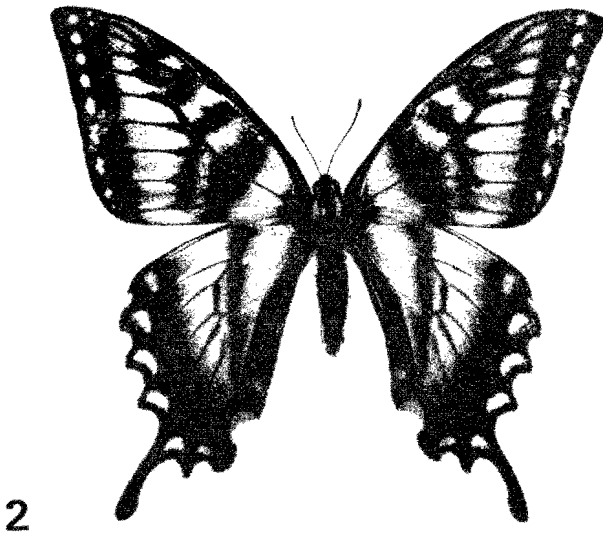
Figure 3.   Dorsal view of another aberrant yellow female *P. glaucus* reared from the female parent (#1372) collected in Green Lake County, Wisconsin by W. Warfield.

Table 1. — Siblings of the aberrant *Papilio glaucus* females.

PARENT	OFFSPRING				
(Brood #)	males	yellow females	dark females	dead pupae	aberrant colored females
1310[a] wild female (Green Lakes Co., WI)	5	13	0	1	1 (Fig. 2)
1372[b] wild female (Green Lakes Co., WI)	31	26	0	2	1 (Fig. 3)

[a]The mother (1310) produced 41 eggs, of which 10 were infertile and 31 became neonate larvae that were reared on black cherry, *Prunus serotina*. Twenty survived to pupation.
[b]The mother (1372) produced 137 eggs, 99 of which resulted in viable larvae (60 survived to pupation). They were on black cherry, *P. serotina*, balsam poplar, *Populus balsamifera*, and paper birch, *Betula papyrifera* and first instar survival was 45/57, 12/12, and 13/19 respectively. All larvae (n = 5) died on tuliptree, *Liriodendron tulipifera* and (n = 6) on *Ceanothis* spp.

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INTERACTION OF INTROGRESSION FROM *PAPILIO GLAUCUS CANADENSIS* AND DIAPAUSE IN PRODUCING "SPRING FORM" EASTERN TIGER SWALLOWTAIL BUTTERFLIES, *P. GLAUCUS* (LEPIDOPTERA: PALILIONIDAE)

J. Mark Scriber[1]

ABSTRACT

The small early "spring form" of the eastern tiger swallowtail butterfly, *Papilio glaucus* has been described from Massachusetts and Illinois in the north, southward all the way into North Carolina. The wing size, shape, patterns, and color all resemble the northern subspecies, *P.g. canadensis*. The possibility was explored that the "spring form" could in fact be a reflection of genetic introgression from the northern subspecies into *P.g. glaucus* populations with laboratory hybrid and backcross studies between *P.g. glaucus* and *P.g. canadensis* under controlled environments on common foodplants. In addition, morphometric multivariate discriminant analyses of 18 wing characters showed that a *P.g. canadensis* genetic component to the 'spring' form could account for much of the wing pattern, size, and shape. Some environmental effects manifested during the diapause stage could also be involved in wing phenotype determination. Both genetic and environmental influences are likely to be involved in the explanation of the "spring form" *Papilio glaucus* throughout eastern North America.

The eastern tiger swallowtail butterfly, *Papilio glaucus* L., occupies the North American continent from Alaska to Mexico east of the Rocky Mountains and is comprised of four putative subspecies: *P.g. arcticus* Skinner, *P.g. canadensis* Rothschild and Jordan, *P.g. glaucus* L., and *P.g. australis* Maynard (Tyler 1975). The taxonomic status of these 4 entities remains uncertain, although individuals from Alaska (*P.g. arcticus*) and *Papilio glaucus canadensis* populations across Canada and north of the Great Lakes hybrid zone (Fig. 1) are physiologically, ecologically, and morphologically distinct from *P.g. glaucus* and *P.g. australis* (Table 1). In addition, females of *P.g. canadensis* and *P.g. arcticus* lack the Y-linked genetic capacity for the dark (melanic) morph observed in some females of *P.g. glaucus* populations from the Great Lakes Region to southern Florida (including individuals from the purported range of *P.g. australis* [Hagen and Scriber 1989]). Furthermore, all *P.g. canadensis* individuals appear to possess a sex-linked dark color suppressor (S +) which is absent in *P.g. glaucus* and *P.g. australis* (Scriber et al. 1987, Hagen and Scriber 1989). Finally, and perhaps most significant, among the biological differences which set *P.g. canadensis* apart from *P.g. glaucus* and *P.g. australis*, is a gene for obligate diapause in *P.g. canadensis* which also is lacking in *P.g. glaucus*

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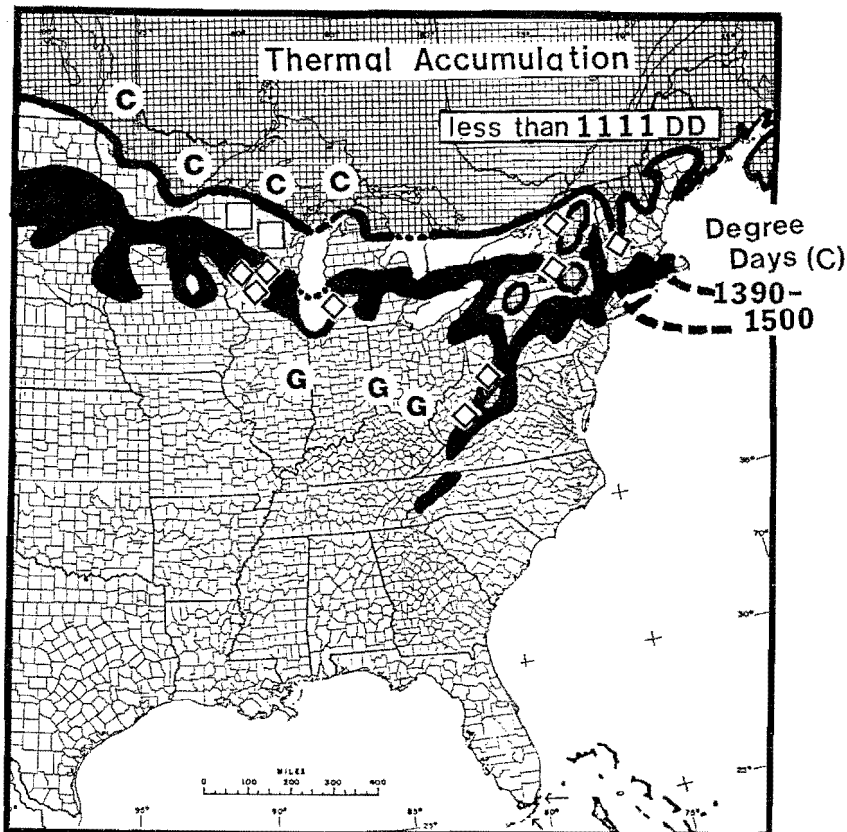
Figure 1. Distribution of selected *Papilio glaucus* populations relative to the seasonal average (20 year) of the thermal unit accumulation above a base threshold of 10°C (50°F) across the Great Lakes and Appalachian Mountain region. The "C" and "G" designate the geographic source of the *P.g. canadensis* and *P.g. glaucus* reference populations used in the multivariate morphometric analyses (see Luebke et al., 1988). The large squares represent 8 counties in northern Wisconsin and the small diamonds represent the potential hybrid populations (all males were computer classified; see Table 2).

and *P.g. australis* (Rockey et al. 1987a, 1987b). It may be that *P.g. canadensis* (which likely includes *P.g. arcticus* [Hagen and Scriber 1990]) warrants status of a separate species (Hagen and Scriber, in prep.).

The northernmost limits to bivoltine populations of *P. glaucus* is delineated by the zone of the thermal unit accumulation between 1390–1500 C degree days above a base temperature of 10°C (2500–2700 F degree days) and also depends upon the particular foodplant (Scriber 1982, Hagen and Lederhouse 1985, Scriber and Hainze 1987). This zone occurs from Minnesota to New England and is characterized by 20 year averages of meteorological data across the eastern half of the United States (see Scriber and Hainze 1987). Within this zone strong selection for univoltinism and obligate diapause would be favored anywhere less than 2500–2600 degree days

Table 1. — Summary of genetic differences between *P.g. glaucus* and *P.g. canadensis*. We are basically convinced that *P.g. arcticus* = *P.g. canadensis* and *P.g. australis* = *P.g. glaucus* (Hagen and Scriber, 1990).

P.g. glaucus trait	*P.g. canadensis* trait	Mode of inheritance	Reference
1. Ldh 100	Ldh 79	x-linked allozyme	Hagen & Scriber 1989
2. Pgd-100	Pgd-125	x-linked allozyme	Hagen & Scriber 1989
3. Hk fast (110)	Hk slow (100)	autosomal allozyme	Hagen & Scriber in prep
4.	Obligate diapause	single locus recessive? x-linked	Rockey et al. 1987a Hagen & Scriber 1989
5. n = 4 fragments (x bal)	n = 3 fragments	cytoplasmic (mt DNA)	Hagen, Smith, Hagen & Smith, in prep
6. Female melanism		single y-linked locus	Scriber et al. 1987 Hagen & Scriber 1989
7.	Melanism suppression	single x-linked locus	Scriber et al. 1987 Hagen & Scriber 1989
8. One-banded larvae	Three-banded larvae	?	Scriber et al. unpublished
9. Tuliptree detoxification		2-4 loci? dominant autosomal?	Scriber 1986
10.	Quaking aspen detoxification	2-4 loci? dominant autosomal?	Scriber 1986
11.	Paper birch detoxification	?	Scriber et al. unpublished
12. Narrow anal wing band	Broad anal wing band	?	Scriber 1988
13. Large adults	Small adults	polygenic?	Luebke et al. 1988
14. Prefers tuliptree for oviposition	Prefers aspen for oviposition	?	Scriber et al. 1990a Scriber et al. 1990b

Table 2. — Multivariate morphometric classification of male *Papilio glaucus* based upon *P.g. canadensis*, *P.g. glaucus*, and hand-paired reciprocal hybrids as reference groups.

Geographic location	Adult flight	Computer classifications (males)		
		canadensis	hybrid	glaucus
8 counties, Northern WI*	(June)	159	1	0
St. Lawrence Co., NY	(June)	7	0	0
Bennington Co., VT	(June)	31	1	0
Madison Co., NY	(June)	5	0	1
Taylor Co., WV	(July)	0	5	2
Clay Co., WV	(July)	0	3	6
Allegan Co., MI	(July)	0	3	2
Green Lake Co., WI (wild)	(June)	8	0	0
Green Lake Co., WI (#1303)	(Late July)	0	5	0
Dane Co, WI**	(July–August)	2	10	62
Richland Co., WI**	(June)	2	5	1

*Bayfield, Washburn, Sawyer, Clark, Wood, Price, Oneida, Marinette.
**Data from Luebke et al., 1988.

obligate diapause would be favored anywhere less than 2500–2600 degree days accumulate because larvae of a second generation would not be able to complete development to the pupal stage before leaf abscision and the onset of winter. On the other hand, there is no obvious reason why *P.g. canadensis* would not be able to

ous effects of warmer temperatures may be involved (Ritland and Scriber, 1985). In fact, the extension of this thermal zone southward in the Appalachian Mountains to Virginia, West Virginia, and Pennsylvania toward the Smoky Mountains may permit introgression of *P.g. canadensis* type genes into adjacent populations throughout much of the mid-latitude regions of the eastern third of the U.S. as well as throughout the Great Lakes Region (Table 2, Fig. 1).

With this possibility of genetic introgression from *P.g. canadensis* over large areas of the U.S. south of Canada, it was of interest to determine whether this might largely explain the occurrence of the morphologically distinct early "spring brood" of various *Papilio glaucus* populations (Clark and Clark 1951, Irwin and Downey 1973, Shapiro 1974, Tyler 1975). The phenomenon of "spring brood" distinctness between the earliest emerging individuals and subsequent summer generations has been previously described in considerable morphological detail (Clark 1932, Clark and Clark 1951). The wing shape, wing size, and many features of wing color patterns are strikingly similar for the early "spring form" of *P.g. glaucus* and for *P.g. canadensis* from Newfoundland to Alaska.

The following is a description of the spring form (Clark 1932):

". . . males are very small with the forewings from 42 mm to 45 mm in length. The hair on the thorax and abdomen is very long, and there is a conspicuous tuft of long hair on the frons.

On the upper surface the black border of the hindwings is narrower than it is in the summer form, and the yellow crescents included in it are larger. The black border of the forewings is slightly broader anteriorly than posteriorly, the reverse being true in the summer form, and the yellow spots included in it are larger. The black abdominal border of the hindwing is usually much broader than the interspace between it and the cell.

On the lower surface the dark margin of the hindwings is markedly narrower than it is in the summer form, and its inner border is a straight instead of a scalloped line; it is much more heavily suffused with light scales than it is in the summer form, and the submarginal crescentic spots are very much larger. On the underside of the forewings the submarginal spots in the black border are larger than in the summer form and are usually confluent, forming a rather broad yellow band with a gently scalloped inner border, though they may be separated at the veins."

A comparison photo with details of each morphometric trait measured or scored in this study can be found in Luebke et al. (1988).

After their 1906 description of *Papilio glaucus canadensis* Rothschild and Jordan wrote that the southern spring specimens of *P.g. glaucus* somewhat resemble the small northern form (*P.g. canadensis*), but indicated that the two could be easily distinguished by the much narrower black abdominal border of the hindwings of *P.g. glaucus* (Clark and Clark 1951). Indeed, this black band on the hindwings can provide an accurate means of distinguishing *P.g. canadensis* and *P.g. glaucus* across their zone of hybridization in Wisconsin (see Scriber 1982, 1988), but this single character is not always sufficient to distinguish the subspecies from their hybrids in this zone. However, multivariate discriminant analyses have increased the precision with which correct identifications can be made of the two subspecies and their hybrids (Luebke et al. 1988). Furthermore, in contrast to Rothschild and Jordan's statement, Clark and Clark (1951) point out that the early 'spring form' of *P.g. glaucus* cannot confidently be determined by any single character, including this dark hindwing band.

Although Hagen and Lederhouse (1985) were unable to find significant differences to allozyme frequences between the 'spring' (early) and 'summer' (late) populations of *P. glaucus* from Ithaca, New York (in the heart of the zone of presumed hybrid interaction), we have noted significant differences in the adult wing characters from 'early' versus 'late' flights elsewhere in the Great Lakes blend zone. In an

attempt to determine if introgression from *P.g. canadensis* rather than a non-genetically based seasonal polyphenism (see reviews by Maudsley 1973, and Shapiro 1984) might be responsible primarily for the production of the 'spring form', a series of laboratory hybrid studies with backcrosses was conducted and multivariate discriminant analyses on several wing characters of the resulting males were used for analyses. Studies of seasonal polymorphism since the 19th century suggested that environmental factors such as temperature and photoperiod might be the "adaptive" cause of the different seasonal morphs in many Lepidoptera (Weismann 1896, see also Oliver 1970, Maudsley 1973, Shapiro 1984).

These studies reported here were designed to elucidate the mechanisms affecting the differential diapause response and eclosion sequence (as well as their potential consequences) in *Papilio glaucus*, especially with regard to the genetic versus seasonal polyphenism alternatives (Müller 1955, Oliver 1970). To determine whether diapause itself (winter conditions) caused the adult wing character differences, or genetic effects from *P.g. canadensis* were involved, controlled environment studies and hybridization studies were concurrently employed.

MATERIALS AND METHODS

Adult females of *Papilio glaucus glaucus* and *P.g. canadensis* were collected from the various field locations (Fig. 1) and allowed to oviposit individually on acceptable foodplant leaves (black cherry and sassafras) kept fresh by water-filled aquapics®. Females were housed in clear plastic boxes (12 cm × 20 cm × 30 cm) heated by a 100 W incandescent lightbulb placed approximately 0.5 m from the boxes. Eggs were removed from leaves after oviposition and neonate larvae were subsequently reared on excised leaves of various species of plants (in 4 cm × 15 cm petri dishes with screened ventilation) to pupation. Larvae were reared in controlled environment growth chambers (at 16:8 photo/scotophase with a corresponding temperature regime of 23.5/19.5°C). Foodplant leaves were kept turgid by use of water-filled aquapics, and changed as needed. A mixture of healthy-looking mature (fully-expanded) leaves and younger leaves were used for neonate studies. After weighing, pupae were individually placed in 14 cm diameter screen cages until adult emergence.

Hand-pairings of lab-reared virgin female butterflies to field-collected or lab-reared males were conducted with the pair hanging in a screen cylinder (approximately 12 cm tall by 14 cm diameter) covered by the top and bottom of a petri dish. Females were subsequently set up in the oviposition boxes as described above and eggs were removed every 2 days. Newly enclosed larvae were individually transferred with a camel hair brush and distributed among the various foodplants and reared to pupation as above. All pupae were allowed to remain under non-diapausing conditions for at least 8 weeks for possible adult eclosion. Pupae that did not produce adults during this time period were stored under refrigeration at 5–7°C until the following spring when they were once again set up for adult eclosion in the screen cages (as above).

Only males were used in these morphometric discriminant analyses because many distinguishing characters are obscured in the melanic (dark) morph of the female *P.g. glaucus*. The reference groups against which these summer- and spring-eclosed adults were run as unknowns were field-captured *P.g. glaucus* (from Illinois and Ohio), field-captured *P.g. canadensis* (from Manitoba, Minnesota, and the Upper Peninsula of Michigan), and various hand-paired laboratory F_1 hybrids (including both reciprocal crosses). Fifteen different wing characters were scored for all individuals and data were analyzed using "Stepwise Discriminant Analysis" — BMDP/PM7 (Dixon and Brown 1979) on a Sperry 1108 computer. Additional details of the methodology can be found in Luebke (1985) and Luebke et al. (1988).

Table 3. — Computer classification based on multivariate morphological analyses of male *P.g. glaucus* captured in two flight periods from the same location in Dane County Wisconsin.

Date of capture	Total (n)	Computer classification		
		P.g. canadensis	"hybrid"	*P.g. glaucus*
'Spring', May/early June	(5)	4	1	0
Summer, August	(19)	0	9	10

RESULTS

Because southern regions of Wisconsin, Michigan, and New York State represent the northernmost limits of the multivoltine life cycle in *P. glaucus* populations (Rockey 1987a, Scriber and Hainze 1987), it was thought that these areas especially might be likely to reflect genetic introgression from the northern *P.g. canadensis* subspecies manifested in 'spring form' morphology. In fact, southern Wisconsin Counties were shown to have all three multivariate classifications *P.g. glaucus*, *P.g. canadensis*, and hybrids (Luebke et al. 1988). A sampling of selected populations from five states across the putative hybrid zone (as delineated by thermal unit accumulations representing the northern limits to multivoltinism) indicated that "hybrid types" occur at all of these locations (except St. Lawrence County, NY) with increased frequency the closer they are to the dark band (1390–1500 degree days °C) indicated in Figure 1.

Of the five individual males captured in Dane County, Wisconsin in May/June ('spring'), four were classified (relative to the basic reference populations) as *P.g. canadensis* with one classified as a hybrid. In contrast, of the August captures (n = 19) from the same Dane Co., Wisconsin location, ten were classified as *P.g. glaucus*, and 9 were classified as hybrids (Table 3). These samples were too small to permit a general conclusion; however, it is clear that some obvious morphological differences were present in these two time periods at the same location.

To assure a mixture of *P.g. canadensis* and *P.g. glaucus* genes, a hand pairing (#628) of a dark daughter of a female *P.g. glaucus* (Pickins Co., SC) with *P.g. canadensis* (Marinette County, WI) was made, and adult males scored in the multivariate technique described. The direct developing individuals (representing the 'summer' flight) scored nearly entirely as F_1 hybrids (n = 12) with only a single individual classification as a *P.g. glaucus*. Of the four males that diapaused and eclosed the following year ('spring' flight), all were classified as pure *P.g. canadensis* (Table 4).

A series of backcrosses was made and the direct developing ('summer') males were compared to the diapausing ('spring') emerging males (Tables 5 and 6). In the backcrosses of hybrid females to *P.g. glaucus* males (#540, #677) and of *P.g. glaucus* females to hybrid males (#255), all three computer classifications were observed (*P.g.c.*, *P.g.g.* and hybrid). There was, however, a difference in the direct (summer) versus diapausing (spring) emerging males, with a strong tendency toward the *P.g.*

Table 4. — Computer classification based on multivariate morphometric analyses of male hybrid offspring from a pairing[1] (#628) of a female *P.g. glaucus* with a male *P.g. canadensis*.

Emergence time	Total (n)	Computer classification		
		P.g. canadensis	"hybrid"	*P.g. glaucus*
'Spring' (diapausers)	(4)	4	0	0
Summer (developers)	(13)	0	12	1

[1] A dark daughter of a dark female collected in Pickens Co., SC (by Ric Peigler) mated to a male *P.g. canadensis* from Marinette Co., WI.

Table 5. — Computer classification based on multivariate morphometric analyses of male backcross offspring of three pairings[1] of hybrids of *P.g. glaucus* × *P.g. canadensis* with *P.g. glaucus* (female parents are listed first).

Pairing type and brood number	Total (n)	Computer classification		
		P.g. canadensis	"hybrid"	*P.g. glaucus*
(Pgg × Pgc) × Pgg				
#540 'Spring' (diapausers)	(38)	7	30	1
Summer (developers)	(18)	0	5	13
#677 'Spring' (diapausers)	(18)	7	11	0
Summer (developers)	(15)	0	13	2
Pgg × (Pgg × Pgc)				
#255 'Spring' (diapausers)	(30)	10	20	0
Summer (developers)	(11)	0	10	1

[1]#540 is a pairing of a hybrid daughter of a *P.g. glaucus* yellow morph mother from Schuykill Co., PA with a male *P.g. canadensis* (from Marinette Co., WI) with a *P.g. glaucus* male from Grant Co., WI.

#677 is a pairing of a yellow daughter from a cross of a dark *P.g. glaucus* female (reared from a dark mother collected in Clark Co., GA) and a male *P.g. canadensis* (from Marinette Co., WI) with a male *P.g. glaucus* from Adams Co., OH.

#255 is a pairing of a yellow daughter of a yellow female *P.g. glaucus* stock obtained from Schuykill Co., PA and a male hybrid (of a *P.g. glaucus* female from Clark Co., Georgia with a male *P.g. canadensis* from Price Co., WI).

Table 6. — Computer classification based on multivariate morphometric analyses of male backcross offspring of two reciprocal pairings[1] of hybrids of *P.g. glaucus* × *P.g. canadensis* hybrids with *P.g. canadensis*. The female of each pairing is listed first.

Pairing type and brood number	Total (n)	Computer classification		
		P.g. canadensis	"hybrid"	*P.g. glaucus*
Pgc × (Pgg × Pgc)				
#500 'Spring' (diapauser)	(5)	5	0	0
Summer (developer)	(2)	0	2	0
(Pgg × Pgc) × Pgc				
#555 'Spring' (diapauser)	(18)	15	3	0
Summer (developer)	(0)	0	0	0

[1]#500 is a pairing of *P.g. canadensis* daughter (of a mother collected in Jackson Co., WI) with a hybrid male son of a yellow mother from Schuykill Co., PA and a *P.g. canadensis* father from Jackson Co., WI.

#555 is a pairing of a hybrid female daughter (of a yellow morph mother from Schuykill Co., PA and a *P.g. canadensis* father from Juneau Co., WI) with a male *P.g. canadensis* from Price Co., WI.

canadensis classification occurring in the spring (Table 5). Of a total 86 backcross males that diapaused ('spring' flight), 24 were scored as pure *P.g. canadensis*, 61 as F_1 hybrids, and only one as a *P.g. glaucus* (Table 4). In contrast, 44 males direct developed ('summer' flight) and none were classified as *P.g. canadensis*, 28 were classified as F_1 hybrids, and 16 were classified as pure *P.g. glaucus* (Table 5).

Of the *P.g. canadensis* male (and reciprocal, female) backcrosses to F_1 hybrids (#500 and #555), no *P.g. glaucus* types were observed in any emergence class. In cross #555 (female hybrid × *P.g.c.* male) all males diapaused and were scored mostly as *P.g. canadensis* (n = 15), with only three as F_1 hybrids (Table 6). In cross #500 (*P.g.c.* female × male hybrid) two males directly developed and were both

scored as F_1 hybrids, whereas the five diapausing individuals were all scored as *P.g. canadensis* in the multivariate discriminant analysis (Table 6).

DISCUSSION

This study of seasonal polyphenism in the eastern tiger swallowtail, *Papilio glaucus*, documents that 'spring form' populations can very closely approach the northern, univoltine *P.g. canadensis* in wing phenotype. The computer classification of each individual illustrated that early flight *P. glaucus* individuals from certain populations within the Great Lakes transition zone (e.g. Green Lakes and Dane Counties, Wisconsin) score more frequently as *P.g. canadensis*, whereas the summer flight from the identical locations score as mostly *P.g. glaucus* or as hybrids (Tables 2 and 3). A follow-up series of classifications was conducted with various known hybrid and backcross hand-pairings of the two subspecies. In these studies, individual siblings were reared under identical conditions with the same foodplant. Comparisons were made between the direct developing (summer flight) versus diapausers ('spring flight') and in all cases, the 'spring' brood (diapausers) scored more toward the *P.g. canadensis* reference group and the "hybrid" form than did the direct developers (Tables 3–5), although sample sizes were small. The backcrosses with more *P.g. canadensis* genes (Table 6) scored closer to the "*canadensis*" type than the backcrosses with *P.g. glaucus* (Table 5), and it is probable that a significant genetic component exists for the multivariate morphometric classification.

There is a strong correlation of pupal weight and wing length in both subspecies of *Papilio* (Fig. 2). The differential effects of allometric growth of smaller versus larger adults could very well explain some of the computer-classified differences in the 'spring' (diapausing) versus 'summer' (direct developing) forms in this study. Even a transformation to remove most of the effects of size as done by Luebke et al. (1988), may not totally correct for allometric difference. Nonetheless, it seems certain that there are a number of genetically induced (as well as environmentally modified) effects on wing morphology, color, and patterns among hybrids of these *Papilio glaucus* subspecies.

While it can be assumed that the genetic control of morphology and growth is likely to be quantitative (Atchley 1983, Leamy and Thorpe 1984), the segregation of hybrid types and the skewed distribution of individuals toward *P.g. canadensis* with diapause and toward *P.g. glaucus* without diapause may also have an environmental component effect. In other words, the physiological processes involved in diapause or the environment itself may affect the pupae in such a way to significantly alter the survival (Sims 1983) or morphology (color, size, shape, and pattern) relative to their non-diapausing siblings (Müller 1955, Oliver 1970). For example, Maudsley (1973) was able to show that chilling pupae of previously diapausing zebra swallowtail butterflies, *Graphium marcellus* (Cramer) during certain early stages of pharate adult development (inside the pupal cuticle) would usually give a spring form adult, whereas chilling of pharate adults in nondiapausing pupae did not. He concluded that diapause may be a prerequisite to the production of spring form butterflies by low temperature, and hence, the lack of the spring form from any second generation (non-diapausing) adults in any particular season. The reasons for this phenomenon remain unclear.

In addition, it was pointed out that adults from unchilled, diapausing pupae were not significantly different from unchilled non-diapausing pupae (Maudsley 1973). In the study presented here with *Papilio glaucus* none of the pupae were chill-treated after adult development started inside the pupae (i.e. the pharate stage) and, based on the results from zebra swallowtails described above, the prediction would be that no differences would occur between unchilled pharate adults from diapausing versus non-diapausing pupae (Maudsley 1973). This clearly was not the case. It is however possible that an effect was exerted upon the diapausing pupae before any
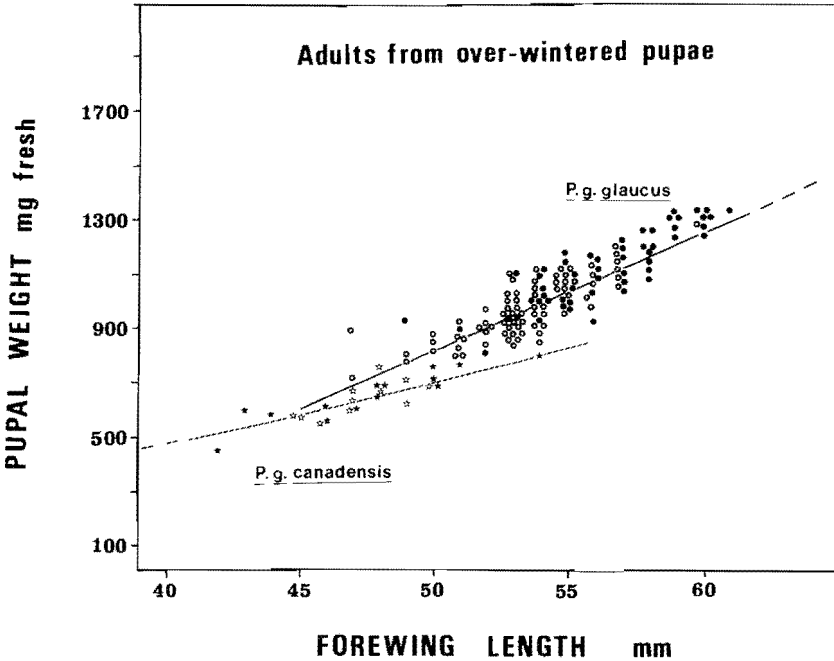
Adults from over-wintered pupae

Figure 2.   The relationship between adult forewing length (nearest mm) and pupal weight (fresh mass) for *Papilio glaucus* (circles) and *P.g. canadensis* (stars). All individuals were from diapausing stock held at 5–7°C in total darkness for approximately 6 months. Females are indicated by solid black symbols, while males are indicated by open symbols.

of the pharate adult development during the winter (dark) storage period (at 5–7°C). This possibility, and the interaction of temperature and photoperiod cannot be ruled out as influencing the spring brood being skewed toward *P.g. canadensis*, however it has been shown here that there is certainly a genetic component from *P.g. canadensis* itself that will also cause this skewing of the spring brood morphotype of *P. glaucus*.

The adaptive significance of male wing size, shape, and pattern has yet to be shown for either the summer form or the spring form of *Papilio glaucus*, however it is known that *P. glaucus* females can discriminate between and preferentially solicit (Krebs 1988) natural males compared to experimentally painted males (Krebs and West 1988). It is possible that size, shape, color, and color pattern of males combined with mate selection by females may be involved in the maintenance of the *P.g. glaucus/P.g. canadensis* hybrid zone across the Great Lakes region.

It is known that the obligate diapause control gene(s) is located on the sex-chromosome (Rockey et al. 1987b). The directly developing males from backcrosses would totally or partially (heterozygous) lack these *P.g. canadensis* (OD +) gene products (Hagen and Scriber 1989). It could therefore be argued that these individuals would also generally have more *P.g. glaucus* traits, while diapausers would generally have more *P.g. canadensis* traits. The experimental *P.g. glaucus* × *P.g. canadensis* male hybrids from brood #628 should have been comprised of equal complements from the 2 parental genomes. Since it turns out that some of these

diapaused and some did not, and that the computer classification scores these direct developers completely differently than the diapausers (Table 3), it is strongly suggestive that there are also some environmental effects involved here and probably in the field as well.

The specific contributions of genetic versus environmental influences still need to be determined to understand fully the specific causes of the 'spring form' of *Papilio glaucus*. For example, in addition to temperature and photoperiod effects on size of pupae, the particular foodplant and/or its nutritional quality have produced different sized siblings. A single female produced offspring with wing lengths ranging from 40–55 mm on *Populus tremuloides*, from 47–57 mm on *Liriodendron tulipifera*, and from 54–65 mm on *Prunus serotina* (all of which occur from Michigan to New England in this Great Lakes hybrid zone shown in Fig. 1). Since allometric effects can be significant in the classification of morphotypes, and since different pupal/adult sizes result from different hosts, it may be that host plant choice in the hybrid zone and Eastern United States is an important nongenetic variable in the occurrence of 'spring form' *Papilio glaucus*.

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BILATERAL DIFFERENTIATION OF COLOR AND MORPHOLOGY IN THE LARVAL AND PUPAL STAGES OF *PAPILIO GLAUCUS* (LEPIDOPTERA: PAPILIONIDAE)

J. Mark Scriber and Robert H. Hagen[1]

ABSTRACT

A sharply delineated, bilateral differentiation of color patterns and morphology were observed in a final (5th) instar larva of a subspecies backcross of a female *Papilio glaucus glaucus* with a hybrid male (*P. g. glaucus* x *P. g. canadensis*). Color and morphological differences were detectable in the pupa as well. In addition, a bilateral size difference was evident in both the pupa and the resulting adult butterfly. Such observations within a single living individual attest to the bilateral independence (also evident in perfect gynandromorphs) and general flexibility of the developmental control in this species of Lepidoptera.

A number of abnormalities have been observed during our laboratory interspecific and intersubspecific hybridization and mass rearing of tiger swallowtail butterflies, *Papilio glaucus* L. We have previously described the occurrence of 39 intersexes (and/or color mosaics) and 3 perfect bilateral gynandromorphs in adult *Papilio glaucus* (Scriber and Evans 1988). In none of these cases did we observe abnormal larvae, nor do we know of the occurrence of bilateral color and/or morphological differentiation in any other larvae or pupae of this species. Such differential bilateral development has been described for larvae of the silkworm, *Bombyx mori* (Tazima 1964). However, larval mosaics may generally be even less frequently noticed and reported than the rare mosaic adults. Here we describe a bilaterally differentiated larva which resulted in a bilaterally distinct pupa and adult *Papilio glaucus*.

MATERIALS AND METHODS

The bilaterally differentiated larva described below is from our general rearing and hand-pairing procedures. While these methods have been described in detail (Scriber et al. 1989), a brief summary is provided here.

Oviposition by adult females is induced by placing each field-captured or lab-paired individual into its own clear plastic box (approx. 10 cm deep x 15 cm x 30 cm) with a moist paper towel and selected foodplant leaves. Heat and light are produced by an incandescent bulb placed at a distance of approximately 0.3–0.5 m from the plastic boxes. Larvae were reared to pupation on foodplant leaves supported in water-filled plastic vials under controlled environmental conditions (18:6 photo-/scotophase at 25°C). Pupae were placed into cylindrical screen cages (15 cm diam-

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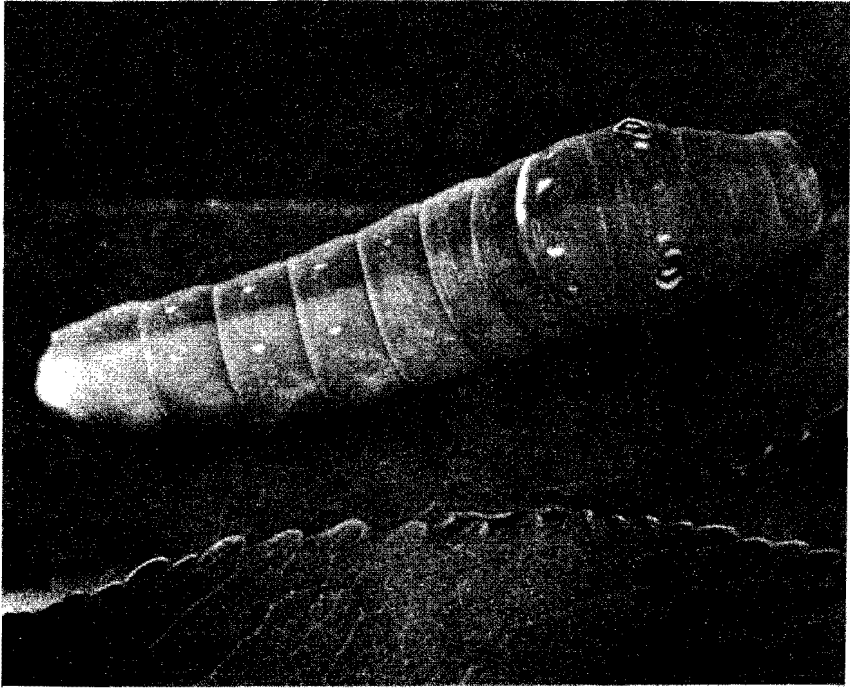
Figure 1.   A bilateral asymmetrical larva (color and morphology) of a subspecies backcross of the eastern tiger swallowtail, *P. g. glaucus*, and the Canadian tiger swallowtail *P. g. canadensis*.

eter x 12 cm height) under larval rearing conditions to permit development and eclosion as adults.

The dark *Papilio glaucus glaucus* mother of pairing #4188 that produced this brood with the bilateral individual was from a Champaign County, Illinois dark mother (provided by May Berenbaum). The 4188 brood father was a hybrid male produced by a pairing of a reared dark female *P. g. glaucus* of a brood from Adams County, Ohio (original collection by Mark Evans and Jeff Thorne) and a male *P. g. canadensis* from Taylor County, Wisconsin.

RESULTS

The left half of this final instar *Papilio glaucus* larva was dark green (normal) and the right half was a bleached lime or yellowish-green color (Fig. 1). In addition, the superanal tubercles were prominent and yellow on the right half (as in many *P. g. canadensis*), compared to the reduced size on the left side (normal *glaucus*-like). The yellow band on the dorsal thorax was prominent on the left half, but not on the right. Otherwise no major differences were noted.

The resulting pupa was bilaterally asymmetrical as well (Fig. 2). The resulting adult (Fig. 3) eclosed with the right side smaller than the left and with minor
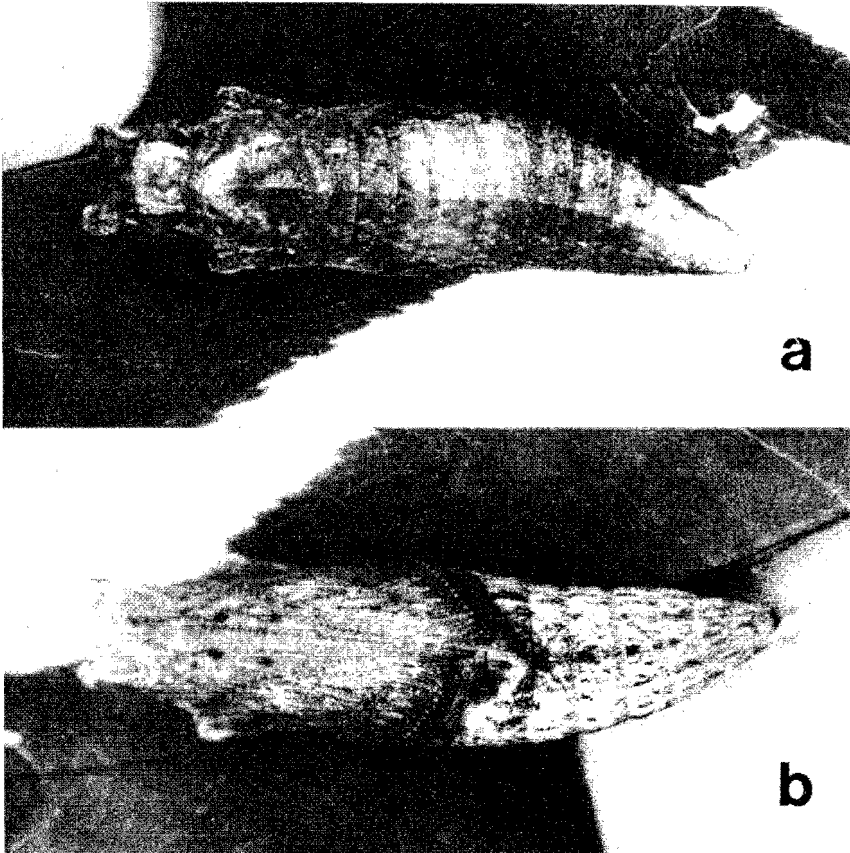
Figure 2.   The dorsal (a) and ventral (b) views of the pupal stage of the same individual (Fig. 1) illustrating the bilateral asymmetry in color and morphology.

morphological differences (in the hind wings especially). The adult appears to be a fairly typical *P. g. glaucus* male (Fig. 3) without obvious evidence of sexual mosaicism or gynandromorphism.

In addition to the bilateral individual, brood 4188 produced one dark morph female and 3 male siblings. These adults all appeared normal in wing pattern. A total of 53 eggs were produced (43 of these were sterile) by the mother of pairing 4188. Seven larvae were reared on wild black cherry to pupation (2 pupae died). Two eggs were fertile but failed to eclose, and one neonate larva died before pupation.

DISCUSSION

This backcross (#4188) that produced this bilaterally distinct individual was also part of a study of the linkage relationships of diapause regulation, color suppres-
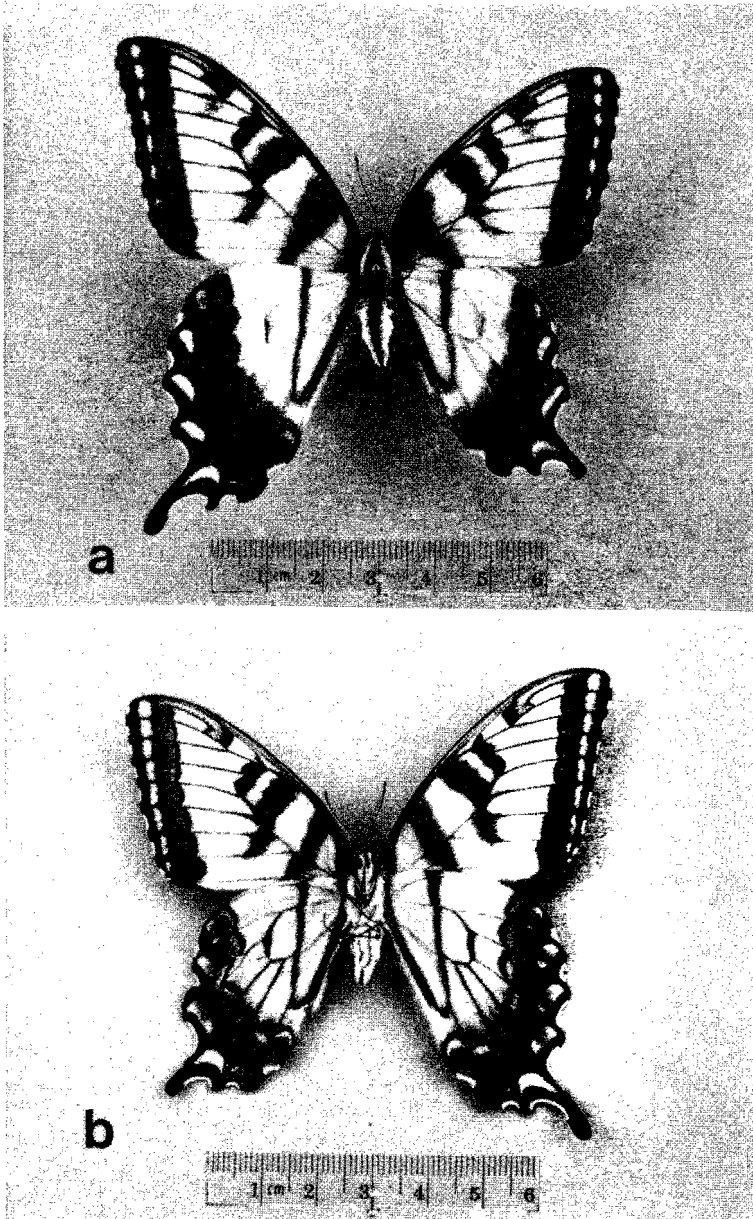
Figure 3.   The dorsal (a) and ventral (b) views of the adult male reared from the same individual as in Figs. 1 and 2.

sion, and allozymes on the sex chromosome of *Papilio glaucus* (Hagen and Scriber 1989). Morphological and color differences exist between the two subspecies (*P. g. glaucus* and *P. g. canadensis*; see Luebke et al.1988). However, it is not clear that this individual is necessarily reflecting subspecific traits in its two halves. This individual is, however, one of a brood that appears to have had recombination of sex-linked (X-chromosome) alleles (Hagen and Scriber 1989). Developmental incompatibilities in *P. g. glaucus* are sometimes introduced from *P. g. canadensis* genes (see Rockey et al. 1987, Scriber and Evans 1986, 1988, Hagen and Scriber 1989) and may have been involved with this bilateral larva.

Developmental processes producing mosaic individuals may result from mono-zygotic fertilization or dizygotic fertilization. Unlike many other animals, insects have embryos of dizygotic origin which can have 2 cell populations fairly easily brought together into a developmental unity (Tazima 1964), resulting in mosaicism (rather than twinning). Several types of mosaics have been described, and it has been noted that the vast majority are bilateral mosaics with contrasting characters mani-fested on both sides of the body divided by the median long axis (Tazima 1964). While such bilaterally differentiated larvae, pupae, and adults may not necessarily be extremely rare, we have, in our *Papilio* rearing efforts over the last decade, handled more than 100,000 larvae and never noticed any others like this one.

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NEW FOODPLANT AND OVIPOSITION RECORDS FOR THE TIGER SWALLOWTAIL BUTTERFLY, *PAPILIO GLAUCUS CANADENSIS* IN ALASKA (LEPIDOPTERA: PAPILIONIDAE)

J. Mark Scriber and Matthew P. Ayres[1]

The eastern tiger swallowtail butterfly *Papilio glaucus* L., is the most polyphagous of all swallowtails (Lepidoptera: Papilionidae) in the world (Scriber 1984). With a geographic range extending from Florida westward into Texas and north to the Brooks Mountain range in Alaska, and eastward across all of forested Canada, it may also have the largest distribution of any of 563 species of swallowtail butterflies in the world. Of several dozen reported host plants, no single foodplant range extends as far as the range of *P. glaucus*. Different local foodplant favorites exist by necessity (Scriber 1986) and with opportunity (Scriber 1988). The extent to which host races (Diehl and Bush 1984) exist across this large geographic range is unknown, however significant genetically-based differences in phytochemical detoxification abilities and survival on various plant species have been noted between the northern (*P.g. canadensis*) and southern (*P. g. glaucus* L.) subspecies (Scriber et al. 1989).

The Alaskan populations of *P. g. canadensis* (sometimes classified as a distinct subspecies *P. g. arcticus* Skinner) have not been extensively studied, and we have been unable to locate any published host plant records for Alaska. Here, we report our field observations of host plant use by the Alaskan *P. g. canadensis*.

We have found eggs and larvae of *Papilio glaucus canadensis* on species of native trees and one introduced tree species in two families (Salicaceae and Betulaceae) in central Alaska in 1988. One the south slope of the roadside (Farmer's road) 3 mi north of the University of Alaska, Fairbanks campus, we found eggs and early instar larvae of the tiger swallowtail on small trees (1–2 m in height). Five balsam poplar, *Populus balsamifera* (Salicaceae), trees were found to have two eggs, a 1st instar larva, a 2nd instar larva and a molting (1st/2nd instar) larva. Two alder trees, *Alnus tenuifolia* (Betulaceae) were discovered which had two eggs and one 2nd instar larva. A small quaking aspen (*Populus tremuloides* [Salicaceae]) sprout had one egg. All of these observations were made on 2 July 1988.

Two days earlier we followed a *P. g. canadensis* female until it oviposited a single egg on the lowest branch of a small quaking aspen tree on the north end of the University of Alaska, Fairbanks campus.

On 4 July, one egg and one 1st instar larva were found on *Salix novae-angliae* (Salicaceae) shrubs near Ballaine Lake (within 1 km of the other observations). These caterpillars were monitored throughout the season, and collected on 3 August as 5th instars (696 and 936 mg fresh mass). The following spring one produced an adult *P. g. canadensis* male while the other turned out to be parasitized by an ichneumonid wasp. Both have been retained as voucher specimens.

On 17 July, in the same vicinity, a 4th instar caterpillar was found on *Alnus tenuifolia*. This was photographed and collected on 28 July as a late 5th instar (1250 mg) caterpillar. It also was parasitized by an ichneumonid wasp.

On 20 July, a 5th instar caterpillar (ca. 500 mg) was discovered on *Betula pendula* (Betulaceae), the European white birch, in a University of Alaska prove-

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nance planting originating from southern Finland. This is particularly notable since we never saw any evidence of oviposition or larval feeding on Alaska paper birch, *Betula resinifera*, which is ubiquitous throughout the area and commonly forms large monospecific stands. The approximately 20 *B. pendula* trees in the birch garden are the only ones we know of in interior Alaska. The natural distributions of *P. glaucus* and *B. pendula* are entirely non-overlapping.

To our knowledge, these observations represent the first records of *Papilio glaucus canadensis* using *Alnus tenuifolia, Salix novae-angliae,* and *Betula pendula* as hosts. Both *A. tenuifolia* and *S. novae-angliae* are abundant in interior Alaska, but their distribution is primarily Beringial and they are not encountered by *P. g. canadensis* in the Great Lakes Region or most of Canada. Conversely, many of the host species reported from the northern Great Lakes region do not occur in interior Alaska. These include black cherry, *Prunus serotina,* chokecherry, *P. virginiana;* and bigtooth aspen, *Populus grandidentata* (Scriber et al. 1982), as well as white ash, *Fraxinus americana* (Scriber 1975); peachleaf willow, *Salix amygdaloides* (Scriber, pers. obs. Emmet Co., MI); lilac, *Syringa vulgaris* and *Carpinus caroliniana* (Shapiro 1974); basswood, *Tilia americana,* mountain ash, *Sorbus americanus* (McGugan 1958, Scriber 1988).

The only host species that appear to be common between interior Alaska and the Great Lakes are *Populus tremuloides* and *P. balsamifera*. Alaskan paper birch, *Betula resinifera,* was long regarded as a variant of *B. papyrifera,* but differs in chromosome number (2n = 56–84 for *papyrifera* vs. 28 for *resinifera*) and is now generally granted species status (Dugle 1966).

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NEW HOST PLANTS FOR ADULT *SYSTENA HUDSONIAS* (COLEOPTERA: CHRYSOMELIDAE) FROM SOUTHWESTERN VIRGINIA

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ABSTRACT

Adults of the flea beetle, *Systena hudsonias*, were observed feeding on *Ambrosia trifida* and eight previously unrecorded host plants in southwestern Virginia. New host plant records for *S. hudsonias* include: *Arctium minus, Aster nova-angliae, Chrysanthemum maximum, Eupatorium fistulosum, Helianthus annuus, Rudbeckia hirta* (Asteraceae), *Mentha spicata* (Lamiaceae), and *Verbena urticifolia* (Verbenaceae).

The nineteen species of *Systena* (Coleoptera: Chrysomelidae: Alticinae) known from North America (Wilcox 1975) feed on a spectrum of herbaceous and woody plants (Blatchley 1910, Balsbaugh and Hays 1972, Wilcox 1979). Some *Systena* species [e.g., *S. frontalis* (Fabricius), *S. blanda* (Melsheimer), and *S. elongata* (Fabricius)] are occasional pests of crops and ornamentals (Arnett 1985), but most are innocuous and little studied.

The biology and host plant relations of *S. hudsonias* (Forster) are poorly known. Adults have been associated with several plants including *Ambrosia trifida* (greater ragweed), *Sambucus* sp. (elder), *Solidago* sp. (goldenrod) and *Zea mays* (corn) (Blatchley 1910, Metcalf et al. 1962, Balsbaugh and Hays 1972, Wilcox 1979). Duckett (1920) also listed wild aster, canna, grape, garden beet, potato and pole beans as hosts for *S. hudsonias*. This species has been called the smartweed flea beetle (e.g., Metcalf et al. 1962), yet there appears to be no published record of *S. hudsonias* feeding on smartweeds (*Polygonum* spp.). *Systena frontalis*, a species that closely resembles *S. hudsonias* (Blatchley 1910), feeds extensively on *Polygonum* (Blatchley 1910, Herrick 1925); thus association of *S. hudsonias* with smartweed could be due in part to misidentification of *S. frontalis*.

During June and July of 1987, 1988, and 1989, I observed adult *S. hudsonias* feeding on several cultivated and wild host plants growing in the ornamental plantings and field margins of a small farm in Blacksburg, Montgomery County, Virginia. Beetles were generally first observed in early June and were common through mid-July in all three years. This pattern of limited seasonal abundance of adults agrees with other published observations for this species in the eastern United States (Kirk 1970, Balsbaugh and Hays 1972, Riley and Enns 1979), and suggests that *S. hudsonias*, like other *Systena* species, is apparently univoltine (Herrick 1925).

Systena hudsonias adults were observed feeding on plants of three families: the Asteraceae (composites), Lamiaceae (mints), and Verbenaceae (vervains). Beetles

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primarily fed on plants in the Asteraceae including *Ambrosia trifida, Arctium minus* (common burdock), *Aster nova-angliae* (New England aster), *Chrysanthemum maximum* (cultivated Shasta daisy), *Eupatorium fistulosum* (hollow Joe-pye weed), *Helianthus annuus* (cultivated sunflower), and *Rudbeckia hirta* (black-eyed Susan). *Mentha spicata* (spearmint) and *Verbena urticifolia* (white vervain) were the only non-asteraceous plants fed upon by *S. hudsonias*. Except for *A. trifida*, all of the above plants are previously unrecorded hosts of *S. hudsonias*. Host plant and insect voucher specimens are deposited in the Virginia Polytechnic Institute and State University herbarium and the Cornell University Insect Collection, respectively.

Feeding beetles generally caused minor damage to plants and, when observed in the field or confined to petri plates with host plant leaves, usually fed on the adaxial surface of leaves. Typical *S. hudsonias* feeding damage consisted of circular scrapes of the leaf surface ca. 1–2 mm in diameter and (or) linear scrapes up to 5 mm in length and 1 mm in width. Beetles were particularly abundant on *A. nova-angliae, M. spicata,* and *V. urticifolia*; these plants grew in close proximity along a stream margin and aggregations of ten or more beetles per plant were commonly observed. Numerous other *Aster* and *Solidago* species also occurred at the stream margin, but *S. hudsonias* was not observed feeding on any of them.

Systena hudsonias is apparently an oligophagous or polyphagous species in southwestern Virginia and in other portions of its wide range (e.g., Quebec to South Dakota and south to Florida and New Mexico [Wilcox 1975]). Plants in the Asteraceae appear to be important hosts for *S. hudsonias*, although the array of plants fed on by this insect may vary with the taxonomic composition of the plant community in which it occurs, and local feeding specializations.

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NATURAL HISTORY OF THE COMMON SOOTY WING SKIPPER, *PHOLISORA CATULLUS* (LEPIDOPTERA:HESPERIIDAE), IN CENTRAL ILLINOIS

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ABSTRACT

The common sooty wing skipper, *Pholisora catullus*, has three broods each year in east-central Illinois. Adults are active for only a few hours at mid-day. Wing color is a rough indicator of age in the field, changing from black to brown over 5 days. These skippers have adult lifespans of about 1 week in the field. Females mate early on their first morning of adult life, and some females mate more than once in their lifetime. Females can lay up to 32 eggs daily, and appear to be able to detect host plants visually over a distance of up to one meter. Densities of these insects are lower in and around urban areas even though larval host plants and suitable nectar sources for adults are present.

The common sooty wing skipper, *Pholisora catullus* Fabricius, is a black or brownish skipper with a variable number of white dots on the forewings. This native skipper is widespread in North America (Klots 1951, Opler and Krizek 1984). In east central Illinois, larvae of this species are often the most frequently encountered leaf-feeding insect on lamb's-quarters (*Chenopodium album*, Chenopodiaceae) in open fields (Capman 1988). This paper reviews my observations on the natural history of this species.

Chenopodium album is an annual plant that generally grows on recently disturbed soil. Its seeds can remain dormant in the soil for 30−40 years (Holm et al. 1977), allowing rapid colonization of newly plowed fields. Mature plants range from several centimeters to more than 2 m in height, depending on growing conditions. There are several similar species of *Chenopodium* that are native to North America (Gleason and Cronquist 1963), and although *C. album* is generally considered to be an introduced species from Eurasia, some archaeological evidence suggests that it may also be native to North America (Johnston 1962).

METHODS AND MATERIALS

Field observations were made over four growing seasons, from 1982 through 1985, in open fields near Urbana, Illinois (Champaign Co.). I seldom saw this skipper in the city even though larval host plants and suitable nectar plants occurred there.

Most work was concentrated at the Ecological Research Area of the University

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of Illinois (Phillips Tract) located about 5 km northeast of Urbana. Habitat types included weedy alfalfa *(Medicago sativa)* fields, weedy bluegrass *(Poa pratensis)* fields, and fields in various stages of secondary succession. I made some observations in an experimental field in which *Chenopodium* plant patches of three sizes (60 cm, 120 cm, or 240 cm diameter) were distributed uniformly, spaced 7 m apart in a 40 m x 100 m area of mowed foxtail grass *(Setaria faberi)*. Results of experiments conducted at this site are reported in Capman et. al. (1990). Additional field observations were made at the Meadowbrook Park community garden plots at the edge of town in south Urbana.

Captive adults were observed in a 9 m x 3.6 m x 2.4 m outdoor flight cage (constructed of a fine nylon mesh [ca. 10 threads/cm] that let most of the sunlight through) erected in a grassy, sunny area between two wings of a building. .

Voucher specimens of *P. catullus* have been deposited at the Illinois Natural History Survey in Champaign, Illinois.

PATTERNS OF ABUNDANCE

Opler and Krizek (1984) report two broods per year, but I consistently observed three broods. At Phillips Tract, the three broods of adults appeared during the spring and summer at roughly monthly intervals, with the population size increasing substantially with each brood. Adults of the first brood occurred in late May and early June, the second occurred in middle to late July, and the last brood in middle to late August. The August brood in particular was very synchronized; the adults appeared over a brief period (2 to 3 days) at the beginning of the two-week flight period and disappeared over a similarly short interval at the end. Generally, the August brood had no stragglers outside of this 2 week flight period.

At Meadowbrook Park the broods were less synchronized. I often found adults at Meadowbrook when none were seen at Phillips Tract even though the *P. catullus* densities were much higher at Phillips Tract. I rarely found *P. catullus* larvae on *Chenopodium* plants at Meadowbrook, but they could be found with only a casual search at Phillips Tract. The reasons for these differences are not clear, but a possible explanation for the differences in synchrony is that adult lifespans may have been longer at Meadowbrook due to a greater abundance of nectar producing plants in the gardens and a greater availability of water due to watering by gardeners.

Larval densities on *Chenopodium* plants growing at Phillips Tract varied with location within the field. I usually found many more larvae per plant on small isolated patches (less than 1 m diameter and at least 5 m away from other *Chenopodium* plants) than on plants growing in large patches (several meters across). Larval densities in August and September ranged from more than ten larvae per plant on small isolated patches to fewer than one larva per plant in very large patches (see Capman et. al. 1990 for additional details). Similar larval dispersion patterns have been described for a number of other butterflies (see Stanton 1983 for a general review of insect dispersion patterns on patchily dispersed host plants).

APPEARANCE AND LIFE HISTORY

Holland (1901), Klots (1951), Opler and Krizek (1984), and, particularly, Scudder (1889) give descriptions of the appearance and life history of *P. catullus* (see Tietz [1972] for additional references). In the summary given below, any unattributed information is based on my observations.

As described by the above authors, *P. catullus* adults are black or brownish skippers with a variable number of white spots on the forewings. These white spots tend to be more numerous on females than on males (Scudder 1889), and I have

found that individuals with very prominent white spots are almost invariably females. The size and number of these spots vary considerably in both sexes, however, and the most reliable way to determine the sex of individuals at a distance in the field is by their flying behavior. Male flight is extremely rapid and erratic. Females usually have a noticeably slower, more fluttery flight, particularly when in the presence of host plants.

The fact that the August brood of adult *P. catullus* appeared abruptly at Phillips Tract made it possible to make rough correlations between age and wing color. For the first few days after adults start appearing, all individuals have the glossy black wing color of newly eclosed adults. After about two days, some individuals have brownish black wings. After about five days, individuals with dull brown wings (that are usually badly frayed) become common (although, as mentioned below, newly emerged individuals are still seen). Thus the approximate age of an individual with glossy black wings is 1 or 2 days, brownish black wings indicate an age of about 3 to 5 days, and dull brown wings indicate the adult is probably 5 or more days old. The wings of individuals held in small cages in the laboratory show roughly the same rate of change in color as seen for adults in the field. Lederhouse (1983) proposed a similar method of estimating the ages of black swallowtail butterflies, *Papilio polyxenes asterius* Stoll, on the basis of wing condition.

Adult *P. catullus* appear to live about a week in the field. This estimate is based on the observation that in August, adults are present for about two weeks, but freshly emerged adults are found only during the first week of this time period.

Pholisora catullus eggs are laid singly on the upper surface of the leaf, generally near the midrib (Scudder 1889). Opler and Krizek (1984) note that the eggs are white or creamy when laid, but I have always observed a muddy brownish-pink color from the moment eggs are laid. Larvae do not eat the eggshells after hatching, and these shells remain on the leaf for at least a week.

Newly-hatched larvae are yellow with black heads; older larvae are green with black heads. They are typical skipper larvae in that their bodies narrow just behind the head and their heads are very large (Scudder 1889). These skippers overwinter as larvae in cocoons (Opler and Krizek 1984). Overwintering larvae take on a slightly pink color in late summer or early fall (Scudder 1889).

Eggs hatch in about 8 days and larvae pupate in the spring and summer after about 17 days. Overwintering larvae, which develop in late August and September when the weather is cooler, take approximately one month to reach full size. The pupation period for spring and summer broods is 7 days.

BEHAVIOR AND REPRODUCTION

On a typical hot sunny summer day, females are active from about 1000 – 1300 h. Males begin flying about an hour before females but stop flying at about the same time as females. On cooler or slightly overcast days, adults do not become active until 1100 h and may continue flying until as late as 1600 h. Opler and Krizek (1984) report similar daily activity periods.

Males appear to patrol for females, circling around and zigzagging across areas a hectare or more in size. They seem to prefer areas with very low vegetation and they commonly follow the borders of mowed fields or pathways that are surrounded by taller vegetation. Males will pursue any dark-colored insect that flies past, whether it is a banded-wing grasshopper (Orthoptera: Acrididae subfamily Oedipodinae), black swallowtail butterfly (*Papilio polyxenes asterius*), or male or female *P. catullus*. Flights in pursuit of insects that are not *P. catullus* females generally end quickly; the males land or fly off after overtaking the insect being chased. Thus, this behavior does not appear to be aggressive or territorial, but rather, that of males searching for mates.

When a *P. catullus* female is being pursued by a male, the two insects flutter

together for a distance of 10 to 40 meters before the female lands. The male then flutters or walks excitedly around her, curling his abdomen toward hers with his claspers spread open. If the female is receptive, copulation occurs almost immediately, otherwise, the female sits with her wings folded and turns frequently to avoid the advances of the male. In such cases, males may persist in their advances for a minute or more before flying away. Patrolling males also frequently detect and attempt to mate with females sitting in vegetation or on the ground. In the flight cage described above, I observed two males each attempting to copulate with the other (their abdomens were curled toward each other with claspers spread).

A female adult emerges from the pupa shortly after sunrise, and will probably have mated by 1000 – 1100 h that same morning. I observed several newly emerged females, which were still sitting near their site of emergence, fly up toward passing males, flutter in the air with them as described previously, and subsequently copulate with them. Thus, a female's first flight is likely to be a mating flight. Although it seems likely that virgin females mate soon after eclosion, matings can be seen in the field as late as 1500 h. Opler and Krizek (1984) report that matings occur between 930 and 1400 h.

Although males frequently attempt to mate with females that are actively searching for host plants and laying eggs, in all cases I observed, such females rejected the male. However, of two females that I dissected and checked for spermatophores, one had two spermatophores in her bursa copulatrix, indicating that multiple matings can occur.

Oviposition and successful larval development occur on both *Chenopodium* and *Amaranthus retroflexus* plants, and an individual female may visit both species during the same bout of oviposition. However, I seldom found eggs or larvae on *Amaranthus* plants, even in areas where *Amaranthus* plants were abundant, suggesting that *Chenopodium* may be the preferred host in central Illinois. Shapiro (1968) has also found larvae on *Celosia argentea* var. *cristata* (cockscomb, Amaranthacae). Opler and Krizek (1984) note that several members of the mint family may be fed upon, but I have not observed this. On several occasions I have observed females ovipositing on *Chenopodium* plants within meters of *Monarda* spp. or *Mentha* spp., but these mints were always completely ignored.

An ovipositing female often lands several times on several different leaves within a patch of *Chenopodium* before laying an egg. At many of these landings, the female curls her abdomen and presses her abdomen tip against the upper surface of a leaf, sometimes dragging her abdomen tip a short distance along the leaf surface. An egg may or may not be laid at this point. The female flies off immediately following oviposition. She may then lay several more eggs in the immediate vicinity or she may fly 10 m or more before resuming oviposition activity (see Capman et. al. 1990 for additional details on oviposition behavior). Females show no obvious tendency to avoid laying eggs on plants or leaves that already harbor eggs.

The inital attraction of female *P. catullus* to host plants appears to be by visual cues. This is suggested by the fact that females initially seen flying in a straight line occasionally veered abruptly toward nearby *Chenopodium* patches. Since these patches were downwind, response to chemical cues seems unlikely. The greatest distance over which this attraction occurred was approximately one meter.

The fact that females often land and drag their abdomen tips along the surfaces of several different leaves before laying an egg suggests that some physical and/or chemical cues are involved in the choice of oviposition sites. This notion is further supported by the fact that on several occasions, individual *Chenopodium* plants had large numbers of eggs (more than 10 per plant) while neighboring plants had no eggs. In these cases, all of the plants in the vicinity looked identical to me, and the branches of the plants were so interwoven that I could not tell which branch belonged to which plant without carefully tracing it to its source.

Three females caught early in the morning before oviposition and three caught in late afternoon after the day's oviposition were dissected and compared to get an

estmate of daily oviposition. These females were all roughly 3 – 5 days old, based on the wing color criteria discussed above. Four ovarioles occurred in each of two ovaries. These ovarioles converged on a median oviduct (there were no lateral oviducts) that was approximately three egg diameters long. In females caught early, there were three to four fully chorionated eggs in each ovariole, plus three chorionated eggs in the median oviduct. In contrast, a total of only three or four chorionated eggs were present in females caught late in the day. Thus, females probably laid between 24 and 32 (8 ovarioles times 3 or 4 eggs per ovariole) eggs daily.

The accessory glands of female *P. catullus* are very large and dark reddish brown in color. Eggs in the median oviduct, soon to be laid (in females caught in the middle of egg-laying), are creamy white in color, but eggs are a muddy brownish pink immediately after being laid. These observations suggest a secretion from the accessory gland coats the eggs as they are being laid.

Very soon after hatching, a first instar larva crawls down the petiole of the leaf to the stem of the shoot, and then upward to the crown of new leaves at the tip of the shoot. The larva webs these young leaves together with silk and stays and feeds in this leaf nest through the first or second instar. As the larva grows larger it makes progressively larger leaf nests. At first, two cuts are made in a leaf edge. The resulting flap is folded over and secured with silk. Later the larva rolls leaves lengthwise or ties together several adjacent leaves. Late in the summer, leaf nests may be constructed by tying together adjacent branchlets of *Chenopodium* inflorescences. The larva spends the day inside the leaf nest and comes out only at night to feed.

During the summer, pupation occurs within loosely woven cocoons (Scudder 1889). Captive larvae spin these cocoons within their leaf nests, in corners of the rearing cage, or among dead leaves on the soil. In the field, it is extremely rare to find pupae within leaf nests, suggesting either that most pupation occurs in leaf litter on the soil, or that mortality rates of last instar larvae are extremely high. Overwintering larvae produce much tougher cocoons made of coarser, darker colored silk (Scudder 1889).

I observed adults of both sexes feeding at several kinds of flowers, including *Sida spinosa* (Malvaceae), white and red clovers (*Trifolium* spp.), and alfalfa (*Medicago sativa*); however, they do not spend a great deal of time feeding. I also observed males gathering at, and apparently drinking water from, puddles and patches of wet mud.

SOURCES OF MORTALITY

When predaceous pentatomid bugs feed on *P. catullus* larvae, the larvae become black and shrivelled. It was not uncommon to find larvae that died in this way in leaf nests on plants in the field, and occasionally I found the bugs in the act of feeding. In addition, on one occasion I saw a vespid wasp cutting open leaf nests and carrying off the larvae.

I found one larva dead in its leaf nest together with a mass of small, white, oval wasp cocoons that appeared to have come from parasitoids that developed inside the caterpillar. These wasps were not reared out and could not be identified.

Survivorship curves for *P. catullus* from eggs through the fourth instar are presented in Capman, et. al. (1990), but the percent mortality caused by each of the above factors is not known.

CAPTIVE REARING

Although it is simple to rear larvae to the adult stage, adult *P. catullus* are extremely difficult to manage in captivity. A few adults survived about five days

when kept in a small plexiglas cage (a plexiglas tube, 11 cm wide x 22 cm long, covered at one end with nylon mesh, and set over a potted *Chenopodium* plant), but no mating or egg laying occurred. Several wild-caught females laid a few eggs when kept in small (100 ml) jars with some *Chenopodium* leaves, but the females lived only about two days.

Although a few individuals mated and laid eggs within the confines of the outdoor flight cage, their behavior was erratic and most individuals died quickly. In nature, *P. catullus* adults spend most of their time flying within a meter of the ground, but adults placed in the flight cage spent most of their time in the upper corners of the cage trying to escape. This resulted in frayed wings, weakening, and death within a day or two of being placed in the cage.

DISCUSSION

The near absence of *P. catullus* in urban areas is puzzling, particularly considering that *Chenopodium* and suitable nectar sources are abundant in town, and the skippers are abundant in the surrounding areas. A possible explanation is that the many physical obstructions in the city might interfere with the natural flight patterns of the adult skippers. Adult *P. catullus* are strong, rapid fliers that traverse large areas very quickly, staying close to the ground at all times. In the field, these skippers will usually try to fly around obstructions such as large shrubs, cars, or buildings rather than flying over them. Just as the confines of the flight cage discussed above interfered with the normal activities of the captive skippers, so might the large number of physical obstructions in urban areas make cities unsuitable habitats for this skipper.

ACKNOWLEDGMENTS

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ADDITIONAL OBSERVATIONS ON *TACHYPOMPILUS FERRUGINEUS* WITH EMPHASIS ON MALE BEHAVIOR (HYMENOPTERA: POMPILIDAE)

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ABSTRACT

An aggregation of 11 males and 5 females of *Tachypompilus ferrugineus* was studied during August and September 1989 at a 2 m-high cemetery monument in Syracuse, NY. Male perching behavior and male-male and male-female interactions are described. Male-male interactions included acceptance, perching in close proximity, wing fanning, circling, following, and flight chases. Overt territoriality was not demonstrated by individual males, although several wasps each maintained a few or several stations. Despite noticeable size variation among wasps, there was no dominant-subordinate hierarchy. Male attachment to the cemetery monument waned as the season progressed due to mortality, increased floral feeding, and decreased female receptivity. Several males often simultaneously pursued an incoming female in an attempt to mate and such males exhibited extensive wing fanning and antennal waving.

In 1989 I presented the first observations on the ecology, mating, and nesting behavior of *Tachypompilus ferrugineus nigrescens* (Banks), a melanic color form that occurs in the northeastern United States. The observations were based upon a study made during mid-summer 1988 at a cemetery monument in Syracuse, NY. These observations led me to conclude that there is no biological validity for separating this subspecies from the more erythritic *T. f. ferrugineus* (Say). During the summer of 1989, I had the opportunity to study the progeny of this aggregation primarily from the standpoint of male activity and behavior rather than female nesting behavior. The results of this study, one of the few on male behavior in pompilids, are presented below.

MALE BEHAVIOR

Males were observed on 1–31 August 1989 between 0950 and 1435 h (EDT) at ambient temperatures of from 19° to 34° C at the same site as described in 1989. They had emerged later in 1989 than in the previous summer (23 July 1988) due to a delayed spring and atypical rainfall pattern and, consequently, their flight season occurred later in the year. As many as 11 males perched simultaneously on the cemetery monument on 4 August 1989; this number was reduced to eight by 10

August and then to five by 15 August. Only three males occupied perches there from 18–23 August and, by 25 August, only a single male was in evidence.

Males perched on the pedestal of the monument in the shaded (E) side in an area 57 cm long and 33 cm wide, 9–42 cm above ground level, except for one wasp that stationed himself on a pile of leaf litter just below an opening in the crevice in which the females were nesting. Six males perched together on 4 August in an area 23 cm long; two pairs of such males perched as close together as 0.6–0.8 cm, often in a head-beside-head attitude, without showing any visible sign of reaction to crowding. A perched male appeared to be alert or ready, as indicated by his slightly raised antennae, outstretched but raised legs and raised body, as opposed to a resting male with legs and antennae outstretched but lowered and body flattened against the stone.

Eleven males perched head downward toward the ground 201 times, following 223 landings on 4 August; these wasps perched head upward only 8 times and head sideways 14 times. Perching following landing by eight males on 10 August revealed similar attitudes: 30 head downward; 4 head upward; 2 head sideways. The head downward perching attitude became less rigid as the season progressed, as exemplified by three males on 21 August: 34, head downward; 12, head upward; 11, head sideways.

Overt territoriality, such as fighting, grappling, instantaneous chasing, or usurpation, was not demonstrated by any of the males. Five of them perched repeatedly on the same protuberances or other raised spots on the pedestal, indicating that some males had preferred stations. Three males returned to their previous perching sites on successive landings. One wasp perched at intervals of 4–28 min on a pile of leaf litter near an opening into the basal crevice (see Kurczewski, 1989) and he returned repeatedly to this site between 4–18 August. He also maintained a few other perches on the pedestal of the monument.

As a male approached the monument in flight, he invariably kept his head oriented toward the stone. Upon landing, he flicked or waved his wings a few times and then held them still but raised at a 35–45° angle for 1–3 sec, as in species of *Episyron* and *Poecilopompilus*, before lowering them flat on the dorsum. This was followed occasionally by rubbing the hindlegs over the back half of the wings and then rubbing the hindlegs together, or cleaning the antennae with the strigili of the forelegs.

Early in the season (1–15 August), males approaching the monument in flight evoked little or no response from males perched on the stone if they landed further away than ±1.0 cm. A resident male often accepted an intruding one and the two maintained perches sometimes only 0.6–1.5 cm apart. If, however, an incoming male landed near (±1.0 cm) a perched male, the two interacted almost immediately. The perched male usually turned, pivoted, or moved sideways to meet the intruder head on or sideways. In 3/4 of male-male close proximity interactions, the resident walked toward the intruder and the two circled one another in a clockwise or counter-clockwise manner, or the resident followed behind the intruder as the latter walked away. Such following of one male by another lasted only 1–2 sec. Sometimes, while circling, the resident male or both males mildly fanned the wings but not overtly so as in the case of a male-female interaction. In 1/4 of the interactions, circling culminated with the resident male chasing the intruder from the monument in a twisting flight which, in turn, often evoked a series of in-tandem flight chases from other males perched nearby. The chasing of one male by another increased per number of interactions as the season progressed and females became less receptive. Late in the season (18–23 August) there was a flurry of flight activity around the monument as resident males landed and took off or chased intruders in flights 2–4 m high.

Despite noticeable variation in the sizes of the males (body lengths, 11–15 mm), there was no visible size-related dominance exhibited by the wasps. Small males followed and chased large males 37 times and vice versa, 39 times. Body size of

males was not correlated with clockwise or counter-clockwise circling behavior. Small and large males circled one another in both directions. Small males maintained 34 perches near the basal crevice in which the females nested and large males, 31 perches. One large male (body length, 15 mm) lived + 21 days while a small male (body length, 12 mm) lived + 23 days. Three different-sized males appeared equally early in the day to maintain perches on the monument; two smaller males appeared at 1041 and 1045 while one larger one made his appearance at 1052 on 18 August.

The number of males seen at the monument decreased from 11 to 1 and they spent increasingly less time there from 1 to 31 August. Male mortality, increased feeding by males at *Daucus carota*, and apparent female unreceptivity are probable reasons for this diminished male activity. Following wasp emergence (1 August), during which males appeared 1–2 days before females, both sexes spent a considerable amount of time at or near the monument. On 4 August (ambient temperature, 34° C) 11 males spent 47 percent of their time at the monument; of this time, 93 percent was spent perching and only 7 percent, walking or flying nearby. On 10 August (25.5° C) seven males spent equal amounts of time perching or walking and flying nearby. On 22 August (22° C), three males continuously landed, perched for 30 sec-1 min, flew away, returned 5–17 min later, perched briefly, etc. During a 30 min-period on 23 August (23° C), three males spent a total of only 6.5 min perched on the monument or walking thereon and 83.5 min elsewhere. Upon leaving, such males flew upward, facing the monument, circled it one or more times, and then made a direct but sinuous flight toward a stand of *D. carota*. Finally, on 28–31 August (21.5°–25.5° C), the last male to be seen flew to the monument at 5–18 min intervals, circled the monument but never landed, flew to other monuments and circled them but did not land thereon.

MALE-FEMALE INTERACTIONS

All male-female interactions observed took place on the pedestal of the monument. Early in the season (1–10 August), males pursued females as the latter landed and entered the basal crevice to nest. Males appeared at the monument earlier in the morning (0950–1040) than the females (1020–1115) and perched near the crevice. A female usually landed on the lawn several minutes after the males had appeared and walked onto the pedestal of the monument, flicking her wings incessantly, at which time one or more males approached her face to face or from the side and began waving their antennae and fanning their wings and possibly producing a sound therewith. Unmated females usually fanned their wings and waved their antennae in response to the male wing fanning and antennal waving, and mating ensued shortly thereafter (see Kurczewski, 1989). Mated (nesting) females were reluctant to copulate but were trailed, often by three or four wing-fanning and antennal-waving males, as they ran into the basal crevice. Other males in the vicinity flew around the female erratically as she ran across the pedestal. Males did not follow females into the crevice. On 4 August, four males trailed and five others flew around a single female as she attempted to enter the crevice. After this female had entered, three males continued to run on her trail, fanning their wings and antennating the area of the pedestal over which she had run. This activity totally disrupted the perching of all 11 males and they eventually flew away after a flurry of flight activity. After 10 min, only one of the males had returned to the pedestal to resume perching at a station.

FEMALE BEHAVIOR

In 1988 females nested within the basal crevice on the W side of the monument which was in sunshine for much of the day (Kurczewski, 1989). In 1989, two females

constructed nests within this crevice on the E and N sides of the monument in a mostly shaded situation. Another wasp enlarged a portion of the crevice on the S side by removing earth and debris to the outside. A fourth wasp nested in an earthen crack in the soil beneath an adjacent smaller tombstone. This female was seen to take inside a piece of dried oak leaf, 0.9 x 1.3 cm, possibly for use as fill.

As in 1988, females returned periodically (9–45 min) to the monument, entered the crevice, sometimes on one side, and exited frequently from another side. Such wasps remained within the crevice for from 1–13 ($\bar{x} = 8$) min; they then usually flew away in a rather straight line, after walking a short distance, and recommenced hunting for prey or, twice, took nectar from the flowers of *D. carota*. Such periodic returns probably served as reorientation to the hunting wasp.

Females hunted for Lycosidae in leaf litter and inside earthen cracks and depressions, 4 m N and 6.5 m W of the monument, from 10 August to 5 September 1989 at ambient temperatures of 22°–33° C. Hunting on the ground surface involved extensive wing flicking, antennation of the substrate, and periodic flights to new hunting areas. One wasp landed on an *Agelenopsis* (Agelenidae) web, ran on it with wings outstretched at about a 45° angle but not flicking upward, and then flew away hurriedly. The occupant of the web was missing.

The prey of one wasp, a *Lycosa rabida* (Walckenaer) (Lycosidae) female, weighing 641 mg, recovered from the effects of the venom and walked away from the depression in which it had been placed.

DISCUSSION

Until rather recently, virtually nothing was known about male behavior in the Pompilidae (Krombein, 1979). Richards and Hamm (1939), Evans (1948), and Evans et al. (1953) noted flight activity of male pompilids and brief encounters between males and conspecific females. Wasbauer (1955, 1957) described several unsuccessful mating attempts by male pompilids in the genus *Anoplius*. He observed that several males often pursued a single female of *A. fulgidus* Cresson and that they became "greatly agitated" when in the vicinity of a female. Barrows (1978) reported patrolling flights and mating attempts of *Evagetes subangulatus* (Banks), a clepto-parasitic spider wasp. He noted that the males did not establish well-defined territories nor did they perch repeatedly on particular landmarks.

In a series of monumental studies, Alcock (1978, 1979, 1981) established that males of the tarantula hawk *Hemipepsis ustulata* Dahlbom defended territories in treetops located high on mountainous ridges. Territory owners were usually larger than conspecific non-territorial visitors. The largest resident males occupied territories closest to the peak of the mountain; smaller males were intruders in these areas or established territories below the preferred mountaintop ones.

In the present study, males of *Tachypompilus ferrugineus* maintained a loose network of stations or perches on an upright cemetery monument but they did not defend these sites vigorously against one another. Lack of overt territoriality in this species may be related to centralization of all activity, both male and female, on an obvious visual landmark. i.e., the cemetery monument. Acceptance rather than aggression was the rule during encounters between conspecific males until midway through the nesting season. Increased aggression between males as the nesting season progressed may be linked to female unreceptivity and their preoccupation with nesting activities. Male station maintenance, i.e., perching, became less rigid with increased female nesting activity and presumed female unreceptivity. Toward the end of the nesting cycle, only a few males were observed perching on the cemetery monument although male mortality may have been the primary reason for this lack of activity.

Early in the nesting season, practically all males of *T. ferrugineus* perched head downward facing the crevice of the monument in which the females nested. As the

number of nesting females increased and they became increasingly unreceptive to male advances, the head downward posture of the males perching on the monument became less rigid, i.e., more males perched in head upward and head sideways attitudes. Males spent increasingly less time in the perched position and more time walking, flying, or obtaining nectar from the flowers of *Daucus carota*.

Shortly after emergence, when nearly a dozen males of *T. ferrugineus* each maintained a few or several stations on the monument, male activity focused on females flying in, landing, and walking into the crevice. Several males usually pursued a single female, waving their antennae and fanning their wings rapidly and possibly thereby producing a sound. Apparently receptive unmated females signalled back to an approaching male with their antennae and wings as they stood face to face or side by side, and mating ensued shortly thereafter with the smaller male positioned atop the larger female (see Kurczewski, 1989). Apparently mated nesting females were reluctant to mate, paid little or no attention to the displaying males, and entered the crevice without hesitation.

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TERRESTRIAL ISOPOD (CRUSTACEA, ISOPODA) SPECIES RECORDED FROM THE GREAT LAKES REGION

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ABSTRACT

Twenty species of isopods have been recorded from the Great Lakes region. Synonymic notes and citations are presented to aid in further research on the isopod fauna of this region.

Not since the work of Van Name (1936, 1940) has there been a source in the literature which summarized the North American distribution records for isopods over a wide geographical region. Therefore as a preliminary step to future studies of terrestrial isopods and their ecological role in the habitats where they are found, we have searched the literature for distribution records from the following states and province: Illinois (IL), Indiana (IN), Michigan (MI), Minnesota (MN), New York (NY), Ohio (OH), Ontario (ONT), Pennsylvania (PA), and Wisconsin (WI). The following list is arranged by family following Harding & Sutton, 1985 and then in alphabetical order by species name. Synonyms used in the publications cited are listed below the currently accepted name. It is not our intent to cite all synonyms for these species, only those used by the authors cited. The source of the record is given following the species name. Where an author cited previous records, we generally used only the original references and did not include secondary citations. Twenty species have thus far been reported from the Great Lakes region. Most authorities (e.g. Hatch 1947, Muchmore 1957) agree that the majority of these species are introduced rather than endemic to the region.

SPECIES LIST

LIGIIDAE

Ligidium elrodii (Packard): IL-Holmquist 1926; IN-Eberly 1953, Underwood 1886; MI-Hatchett 1947, Pearse 1910; NY-Richardson 1905; ONT-Judd 1965, Underwood 1886, Walker 1927
    L. hypnorum Cuv: Holmquist 1926, Underwood 1886
    L. longicaudatum Stoller: Eberly 1953, Hatchett 1947, Judd 1965, Pearse 1910, Richardson 1905, Walker 1927

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TRICHONISCIDAE

Androniscus dentiger Verhoeff: ONT-Van Name 1940
  Trichoniscus (A.) d. Verhoeff: Van Name 1940

Haplophthalmus danicus Budde-Lund: IN-Eberly 1953, Richardson 1905; NY-Muchmore 1957; ONT-Judd 1965, Walker 1927
  H. puteus Hay: Richardson 1905

Hyloniscus riparius (Koch): NY-Muchmore 1957; PA-Schultz 1965; WI-Jass & Klausmeier 1987

Miktoniscus barrai Vandel: IN-Schultz 1976

Miktoniscus medcofi (Van Name): IL-Van Name 1940; IN-Schultz 1976; NY-Muchmore 1957; OH-Muchmore 1964, Schultz 1976
  M. ohioensis Muchmore: according to Schultz 1976
  Trichoniscus (Miktoniscus) medcofi Van Name: Van Name 1940
  Trichoniscus sp. Eberly 1953: according to Schultz 1976

Trichoniscus pusillus (Blake): IN-Eberly 1953; MI-Hatchett 1947; NY-Lohmander 1927, Muchmore 1957; ONT-Judd 1965, Underwood 1886, Walker 1927; PA-Lohmander 1927, Schultz 1965, Van Name 1936; WI-Jass & Klausmeier 1987
  T. pusillus Brandt: Lohmander 1927, Underwood 1886, Walker 1927
  T. demivirgo Blake: Eberly 1953, Hatchett 1947, Judd 1965, Muchmore 1957, Van Name 1936

Trichoniscus pygmaeus Sars: IL-Van Name 1940; NY-Muchmore 1957

ONISCIDAE

Oniscus asellus Linneaus: IL-Richardson 1905; MI-Hatchett 1947; MN-Sargent 1973; NY-Muchmore 1957, Neuhauser & Hartenstein 1978, Richardson 1905; ONT-Judd 1965, Underwood 1886,Walker 1927; PA-Richardson 1905, Underwood 1886
  O. affinis Say: Underwood 1886
  O. vicarius Stuxberg: Underwood 1886

PHILOSCIIDAE

Philoscia muscorum (Scopoli): NY-Schultz 1974

Philoscia vittata Say: NY-Richardson 1905, Schultz 1974

PLATYARTHRIDAE

Platyarthrus hoffmannseggi Brandt: NY-Muchmore 1957

ARMADILLIDIIDAE

Armadillidium nasatum Budde-Lund: IL-Van Name 1936 & 1940; IN-Eberly 1953; MI-Hatchett 1947; MN-Sargent 1973; NY-Muchmore 1957, Neuhauser & Harten-

stein 1978, Richardson 1905, Van Name 1936; ONT-Judd 1965, Van Name 1936, Walker 1927; PA-Hatch 1947.

    A. quadrifrons Stoller: Richardson 1905, Walker 1927

Armadillidium vulgare (Latreille): IN-Eberly 1953; MI-Hatch 1939, Hatchett 1947; MN-Sargent 1973; NY-Muchmore 1957, Neuhauser & Hartenstein 1978, Richardson 1905, Underwood 1886; OH-Richardson 1905; ONT-Judd 1965, Walker 1927; PA-Schultz 1965; WI-Jass & Klausmeier 1987

    A. pilulare Stuxberg: Underwood 1886

CYLISTICIDAE

Cylisticus convexus (DeGeer): IL-Richardson 1905; IN-Eberly 1953; MI-Hatch 1939, Hatchett 1947, Pearse 1910, Richardson 1905; MN-Sargent 1973, Van Name 1936; NY-Fitch 1856, Muchmore 1957, Richardson 1905; OH-Richardson 1905; ONT-Hatch 1939, Judd 1963 & 1965, Underwood 1886, Walker 1927; PA-Hatch 1947, Schultz 1965; WI-Jass & Klausmeier 1987

    Porcellio convexus Johnsson: Underwood 1886

PORCELLIONIDAE

Porcellio laevis Latreille: NY-Van Name 1936; OH-Richardson 1905, Van Name 1936; ONT-Hatch 1947

Porcellio scaber Latreille: IL-Fitch 1856, Richardson 1905; IN-Eberly 1953; MI-Hatch 1939, Hatchett 1947, Richardson 1905; MN-Sargent 1973; NY-Muchmore 1957, Neuhauser & Hartenstein 1978, Richardson 1905, Van Name 1936; OH-Fitch 1856, Richardson 1905; ONT-Judd 1965, Walker 1927; PA-Hatch 1947, Underwood 1886; WI-Jass & Klausmeier 1987

    P. niger Say: Underwood 1886

Porcellio spinicornis Say: MI-Hatch 1939, Hatchett 1947; MN-Sargent 1973; NY-Fitch 1856, Muchmore 1957, Richardson 1905, Van Name 1936; ONT-Judd 1965, McQueen 1976, Underwood 1886, Walker 1927; WI-Jass & Klausmeier 1987

    P. pictus Brandt: Underwood 1886

    P. vittatus Fitch: Fitch 1856

Porcellionides pruinosus (Brandt): IL-Fitch 1856; IN-Eberly 1953; MI-Hatch 1939 & 1947, Hatchett 1947; MN-Hatch 1947, Sargent 1973; NY-Fitch 1856, Muchmore 1957; OH-Richardson 1905; ONT-Judd 1965, Walker 1927; WI-Jass & Klausmeier 1987

    Metoponorthus p. (Brandt): Muchmore 1957, Richardson 1905, Walker 1927

    Porcellio immaculatus Fitch: Fitch 1856

TRACHELIPIDAE

Trachelipus rathkei (Brandt): IL-Cole 1946, Hatch 1947, Holmquist 1926, Rapp 1988; IN-Eberly 1953, Hatch 1939, House 1911; MI-Hatch 1939, Hatchett 1947, Pearse 1910 & 1913, Richardson 1905; MN-Sargent 1973; NY-Fitch 1856, Muchmore 1957, Richardson 1905, Underwood 1886; OH-Richardson 1905; ONT-Hatch 1939, Judd 1963 & 1965, McQueen 1976, Pearse 1913, Rapp 1988, Underwood 1886, Walker 1927; PA-Hatch 1947; WI-Jass & Klausmeier 1987

Porcellio limatus Fitch: Underwood 1886
Porcellio mixtus Fitch: Fitch 1856
Porcellio r. Brandt: House 1911, Pearse 1910 & 1913, Richardson 1905, Walker 1927
Porcellio trilineatus Koch: Underwood 1886
Tracheoniscus r. Brandt: Eberly 1953, Holmquist 1926, Judd 1963 & 1965, McQueen 1976, Sargent 1973

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FIRST SCARAB HOST FOR *STRONGYGASTER TRIANGULIFER* (DIPTERA: TACHINIDAE): THE DUNG BEETLE, *APHODIUS FIMETARIUS* (COLEOPTERA: SCARABAEIDAE)[1]

Foster Forbes Purrington[2], Daniel M. Pavuk[2], Rupert P. Herd[3],
and Benjamin R. Stinner[2]

ABSTRACT

We report *Strongygaster (=Hyalomyodes) triangulifer* as a solitary primary parasite of the adult introduced dung beetle, *Aphodius fimetarius*. This is the first record of this tachinid fly parastizing scarabs.

The Old World dung beetle, *Aphodius fimetarius* (L.) (Coleoptera: Scarabaeidae), is globally distributed in temperate zones. In northeastern Ohio this species is ubiquitous and can be very numerous locally. Adults of both sexes are distinctive among introduced and native Aphodiini by their bright red elytra, black head and pronotum, and large size: to 8.5 mm (Blatchley 1910). They reproduce in the dung of many herbivorous mammals, especially cattle, and in moist litter. Colonizing adults tunnel extensively and oviposit in drying dung pats; larvae develop in cells within the pat. According to Mohr (1943), *A. fimetarius* is essentially univoltine; adults overwinter in dung, oviposit in spring, and produce an autumn adult cohort.

We obtained ca. 200 adult *A. fimetarius* in mid-April 1989 from overwintered cattle dung pats in a wooded pasture near Apple Creek, Ohio (Wayne Co.). They were held individually in plastic 30 ml cups at room temperature and 60% RH. Eight of these captive beetles produced a single fly larva each. From puparia that subsequently formed, adult tachinid flies eclosed in five days (ca. 5 May 1989) and were identified by the USDA Systematic Entomology Laboratory as *Strongygaster (=Hyalomyodes) triangulifer* (Loew).

This New World fly typically parasitizes only adult insects [Thompson (1954) viewed reports of larval parasitism as abnormal occurrences]. Previously reported hosts span a broad phylogenetic range that includes Orthoptera, Dermaptera, Hemiptera, Coleoptera, and Lepidoptera (Lange 1950, Sabrosky and Braun 1970, Smith and Kok 1983, Kevan and Koshnaw 1988). Our record is the first of such parasitism in a scarab, and with it nine beetle families now contain reported hosts for *S. triangulifer* (Table 1).

Table 1. — Beetle families containing reported hosts for *Strongygaster triangulifer* (Loew).

BEETLE HOST FAMILY	REFERENCE
Scarabaeidae	(this report)
Lampyridae	Sabrosky and Braun 1970
Cleridae	Turnbow and Franklin 1979
Meloidae	Cortés and Hichins 1969
Alleculidae	Thompson 1954
Nitidulidae	Williams et al. 1981
Coccinellidae	Thompson 1954, Wellso and Hoxie 1969
Chrysomelidae	Thompson 1954, Sabrosky and Braun 1970, Wellso and Hoxie 1969, Herzog 1977.
Curculionidae	Thompson 1954, Sabrosky and Braun 1970

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TYPOCERUS DECEPTUS IN SOUTHERN ILLINOIS
(COLEOPTERA: CERAMBYCIDAE)

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ABSTRACT

The lepturine cerambycid *Typocerus deceptus* is reported from southern Illinois for the first time. It was collected in association with *T. v. velutinus* near, or in oak-hickory forest stands on *Hydrangea arborescens,* a new host plant record.

Typocerus deceptus was originally described by Knull (1929) from a small series of specimens collected in Pennsylvania. He collected it on *Rhus glabra* during July in Ohio but stated it was never common. Linsley and Chemsak (1976) added Indiana, Virginia, and South Carolina as new state records and found *T. deceptus* on *Rhus glabra* during June and July. Bouseman (1977) listed it from Kankakee, Mason, and Tazewell counties in north-central Illinois, and collected it on flowers of *Ceanothus americanus* and *Cornus* sp. during June and July, and felt that oak-hickory forest stands were used by larvae as host sites. Gosling (1981, 1983) collected it in St. Joseph County, Michigan on flowers of *Ceanothus americanus, Cephalanthus occidentalis, Rosa palustris* and *Daucus carota* during July and near oak-hickory forest stands. Gosling (1981) also found *T. deceptus* in copula and determined that *T. v. velutinus* (Olivier)(nearest sibling) was much more common (ratio of 11.7 *T. v. velutinus* to 1.0 *T. deceptus*).

MATERIALS AND METHODS

At irregular intervals, beginning in 1985, lepturine cerambycids occurring on *Hydrangea arborescens* were collected at Bell Smith Springs and Lusk Creek, Pope County. In addition, an extensive field study of lepturines occurring on *H. arborescens* and *Daucus carota* was conducted in the LaRue-Pine Hills Ecological Area, Union County, during 1987–1988. Both counties are located in southern Illinois. All specimens of *T. deceptus* are deposited in SIUC Entomology Collection.

RESULTS AND DISCUSSION

Thirty-one *Typocerus deceptus* were collected at the three localities. They were collected only on flowers of *H. arborescens* and only during June (N = 18) and July (N = 13), even though extensive collecting was conducted during the flowering period (June and July) of *D. carota* at LaRue-Pine Hills Ecological Area during 1987–88. At no time were any *T. deceptus* found in copula although *T. v. velutinus,*

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occurring with it on flowers, was commonly found mating. All specimens were found in or near oak-hickory forest stands and always in association with *T. v. velutinus*. At the LaRue-Pine Hills Ecological Area, *T. v. velutinus* was most abundant (N = 152), followed by *T. deceptus* (N = 31), *T. lugubris* (Say) (N = 9), and *T. acuticauda* Casey (N = 3). The *T. deceptus* sex ratio was 1.21 ♂:1 ♀.

Results of this study have shown *T. deceptus* present in southern Illinois and associated with *H. arborescens*; it was not found on D. carota. All host records were on plants associated with oak-hickory forest stands supporting results of Bouseman (1977) and Gosling (1981,1983). At no time were any *T. deceptus* collected or sighted in copula as Gosling (1981) found.

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HILLTOPPING BY MALES OF *EUPEODES VOLUCRIS* (DIPTERA: SYRPHIDAE)

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ABSTRACT

Hilltopping, station taking, territoriality, and possibly lek formation are combined to form the mate-locating strategy of *Eupeodes volucris*.

On 25 May 1964, I found a loose assemblage of many males of *Eupeodes volucris* Osten Sacken (Diptera: Syrphidae) at Sand Ridge State Forest in central Illinois, about 20 km NE of Havana. The flies were near the base of a fire tower that was then atop the highest hill in the vicinity. From 1300–1400 h CDT, I took 22 males from this assemblage, and from 1745–1800 h I took another 12. All collected flies were males; no females were collected or seen. I have seldom taken *E. volucris* under other circumstances, either at Sand Ridge or in other parts of central Illinois. Although I have collected here for many years, I have taken only five other specimens of *E. volucris* in central Illinois, all from flowers: two males from the blossoms of *Rosa* spp. and one male and two females from the blossoms of *Pastinaca sativa*, all between mid-May and early July.

The hilltop tower at Sand Ridge was surrounded by open woodland. Medium-sized oaks provided a loose canopy, but there was little or no underbrush. On the day the collection was made, it was clear and hot. The sun shone through the canopy, and the ground beneath was a mosaic of shaded and sun-lit areas.

The males hovered beneath the canopy, usually over a narrow dirt track or other bare areas between the trees. A few hovered as low as ca. 60 cm above the ground, a few as high as ca. 6 m, but most of them hovered at elevations of about 1.5 m to 2.5 m. The horizontal distance between neighboring males varied, but they were generally separated by at least 1 m and seldom by more than 2 m or 3 m. Since the flies generally maintained their positions relative to the ground, it is probable that they were taking a visual fix on some stationary marker either above or below them. The edge of one of the bare areas seems too extensive to have served as the sole marker, but no other tangible markers such as stones or other obects were evident on the ground. It may be that a cluster of leaves or a sunlit spot served as a marker, but the pattern of leaves above the flies and the mosaic of light and shade beneath them were too complex to permit ready identification of either as markers.

Males occasionally interacted with each other. If one male approached another, there was brief contact, but they soon separated and resumed hovering. On occasion, as many as four males came together in an apparently aggressive encounter.

Among the behaviors involved in mate location by insects are: station taking, in which a male watches for females from a vantage point such as a leaf or the trunk of

a tree or as it hovers over or under some visible marker (Downes 1969); territoriality, in which a male defends the area around his station from conspecific males or insects of other species (Wellington and Fitzpatrick 1981, Fitzpatrick and Wellington 1983); hilltopping, in which both sexes orient to some high topographic feature, and the males take stations there (Alcock 1987) (Hilltopping by other Syrphidae was described by Chapman [1954].); and lek formation, in which several males compete for females as they defend small territories within an arena that offers the females no resource other than the males themselves (Alcock 1981). The observations reported above suggest that these behaviors, with the possible exception of lek formation, are combined in the mate locating-strategy used by *E. volucris*. Whether or not lek formation was involved depends upon whether or not this hilltop area offered female *E. volucris* some resource other than conspecific males. Pollen and nectar were virtually absent because there were almost no blossoms on the hilltop. Whether or not oviposition sites were present is not known.

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OCCURRENCE OF *HELOPHORUS GRANDIS* (COLEOPTERA: HYDROPHILIDAE) IN NORTH-CENTRAL WISCONSIN[1]

William L. Hilsenhoff[2]

ABSTRACT

Two males of the Palaearctic *Helophorus grandis* were collected in northern Wisconsin, constituting a significant westward extension of its previous range in eastern Ontario, eastern New York, and areas farther east.

On July 18, 1989, a male *Helophorus grandis* Illiger, 1798 was collected from a small wetland in north-central Wisconsin. This represents a significant range extension for this distinctive species, which previously was known only from New Brunswick, Nova Scotia, Quebec, Ontario (east of Lake Huron), Maine, New Hampshire, and eastern New York (Smetana 1985, 1988). *Helophorus grandis* is the largest *Helophorus* in North America and the only representative of the Palaearctic subgenus *Helophorus* that is known to occur here. It apparently was introduced to the Atlantic coast from Europe late in the nineteenth century, with early collections being confined to Quebec and Maine (Smetana 1985). Its occurrence in Taylor County, Wisconsin, 13 km east of the city of Medford, was unexpected, and suggests that this species should be looked for in northern areas of the western Great Lakes region.

The discovery of *H. grandis* in Wisconsin is probably due to a recent westward movement of the species rather than a lack of collecting. I have used nets and traps to sample various wetlands in all areas of Wisconsin, and have collected more than 54,000 Hydrophilidae, including 2,850 *Helophorus* (13 species). Additional efforts to collect *H. grandis* from the Taylor County site on September 20, 1989 and May 4, 1990 resulted in the collection of another male on May 4. Collection records published by Smetana (1985) suggest that this species is most abundant in the spring and almost completely absent after August. *Helophorus orientalis* Motschulsky and *H. sempervarians* Angus were also found at the Taylor County site in both 1989 and 1990; additionally *H. angusticollis* d'Orchymont was collected there June 22, 1983, the only other time this site was sampled. Other water beetles found at this site are all among the more common and widespread species found in Wisconsin, suggesting that there is little that is unique about this habitat.

Smetana (1988) describes the habitat for *H. grandis* as "temporary pools and the muddy or weedy margins of ponds and lakes". The wetland where *H. grandis* was collected is about 70 meters by 20 meters, heavily vegetated by cattails (*Typha latifolia*) and woolgrass bullrushes (*Scirpus cyperinus*), with a small area of open water in the center that contains some *Ranunculus* and *Lemna*. Maximum water

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depth in 1989 was about 0.5 m, but because of a severe drought in 1988 and below normal rainfall in 1989 this depth was probably about one-half meter below normal. It is quite possible that this habitat became dry in 1988 and was reflooded in 1989 by water from melting snow. The wetland is located along the edge of County Highway C, 1.4 km north of State Highway 64, and is surrounded by a mixed hardwood forest in an area of farmlands intermixed with forests.

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COVER ILLUSTRATION

Mimesa cressonii Packard (Hymenoptera: Sphecidae), provisioning her nest
with a leafhopper.
Photograph by Roy A. Norton