

LATITUDINAL VARIATION IN PHOTOPERIODIC INDUCTION OF PUPAL DIAPAUSE IN THE SPICEBUSH SWALLOWTAIL BUTTERFLY, *PAPILIO TROILUS* (LEPIDOPTERA: PAPILIONIDAE)

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ABSTRACT.— The influence of photoperiod on the induction of facultative diapause was determined for a southern Ohio population of *Papilio troilus*. We also investigated the extent of population differences in critical photoperiod for induction of diapause for Michigan, Georgia/South Carolina, and Florida *P. troilus*. Larvae from several families from each population were reared from neonates to pupae under varying photo:scotoperiods on sassafras or red bay foliage with other conditions held constant. The critical photoperiod for diapause was between 14.0 and 14.5h of light in the Ohio population. This compares with 14.5-15.0h for southern Michigan population, 13.5-14.0h for the Georgia/South Carolina population and 12.0-12.5h for the Florida population. Some family to family variation in response to photoperiod cues was observed. However, a clear general pattern of higher latitude populations having longer critical photoperiods was evident.

KEY WORDS: clines, diapause induction, Florida, Georgia, latitudinal cline, Michigan, Nearctic, North America, Ohio, photoperiod, physiological ecology, USA.

Swallowtail butterflies in the subfamily Papilionidae are able to withstand temperate or arctic winters as diapausing pupae (Kukal *et al.*, 1991). Temperature, food, quality, moisture, and photoperiod all may play a role as token stimuli in inducing diapause in multivoltine swallowtail species (Beck, 1980, 1983; Tauber *et al.*, 1986). Although token stimuli may not influence larval growth themselves, they indicate that a change in environmental conditions is forthcoming. The token stimulus most widely used by insects is photoperiod (Tauber *et al.*, 1986; Danks, 1987). The critical photoperiod for diapause is that photoperiod which induces 50% of a population to enter diapause, given other constant conditions (Tauber *et al.*, 1986).

In species such as *Papilio canadensis* Rothschild & Jordan (Hagen *et al.*, 1991), pupal diapause is "obligate" regardless of environmental cues (Scriber, 1982; Hagen and Lederhouse, 1985; Rockey *et al.*, 1987a). The obligate diapause gene of *P. canadensis* (Rockey *et al.*, 1987b) obviously benefits individuals of this species (Roff, 1980), since the growing season throughout its range is too short to permit more than one generation each year (Scriber and Lederhouse, 1992). The cold tolerance of diapausing *P. canadensis* pupae may be a crucial factor allowing the northern distribution of this species to reach Alaska (Kukal *et al.*, 1991). In *P. glaucus* Linnaeus, diapause is environmentally determined. Larvae that experience long daylength, good quality food, and warm temperatures are much more likely to develop directly into adults than are larvae that experience short days, poor food, or low temperatures (Hagen and Lederhouse, 1985; Rockey *et al.*, 1987a; Scriber, 1994, 1996a). However, obligate diapause would be highly disadvantageous for *P. glaucus*, since it occurs in areas where the growing season should permit 2 or more generations per year (Taylor, 1980a, 1980b).

The geographic distribution of *Papilio troilus* Linnaeus in eastern North America (Scriber, 1996b) coincides closely with the composite range of its native lauraceous hostplants, sassafras (*Sassafras albidum* (Nutt.) Nees), spicebush (*Lindera benzoin* (L.) Blume), and red bay (*Persea borbonia* (L.) Spreng.) (Opler and Krizek, 1984; Nitao *et al.*, 1991; Lederhouse *et al.*, 1992; Frankfater and Scriber, 1999). All known populations of *P. troilus* are multivoltine producing three (or more; Scriber *et al.*, 1998) gener-

ations a year in the south and two generations in the north. However, Opler and Krizek (1984) state that some pupae from each generation overwinter. All Indiana *P. troilus* larvae reared under a 11:13 photo:scotoperiod by Hazel and West (1983) diapaused as pupae but none reared under at 15:9 photo:scotoperiod did.

The purpose of this study was to determine the critical photoperiod for inducing diapause in *P. troilus* for an Ohio population. We also investigated variation in response of different populations in relation to latitude since generally higher latitude populations of insects have longer critical photoperiods (Danks, 1987). This is not always true, especially in area where voltinism (# broods per year) vacillates (Gomi, 1997).

MATERIALS AND METHODS

The southeast Ohio population of *Papilio troilus* (38°-39°N latitude) was sampled from Scioto and Adams Counties, Ohio in July 1991 and Lawrence County in August 1992, and Lawrence County in August 1993, late July and early August 1994, and August 1995. Other populations of *P. troilus* were analyzed for comparison with Ohio. We collected females in Michigan from St. Joseph County (latitude 42°N) in August 1993, and Ingham County (latitude 43°N) in July 1994. Females also were collected in Clarke County, Georgia in August 1994 and Aiken County, South Carolina in 1995 (latitude 32°-33°N). Florida population samples were derived from females collected during late March in Highland County in 1993 and Highlands and Levy Counties (latitude 27°-28° N) in 1994 and 1995. To control as much as possible for maternal age effects (Mousseau, 1991), we used only the youngest females from our field captures.

Ovipositing females were fed a 1:4 solution of honey and water. Eggs were collected daily and put in a 24°C (1991 and 1992) or 18°C (1993-1995) chamber with a 18:6 photo:scotoperiod until hatching. Neonate larvae of each female were distributed equally across treatments but in random order. Florida populations were reared on red bay, *Persea borbonia*, their only natural host (Nitao *et al.*, 1991). Georgia, Ohio and Michigan larvae were reared on one of their common hosts, *Sassafras albidum* (Lederhouse *et al.*, 1992).

In the 1991 Ohio experiment, larvae were reared at a constant 24°C under three photo:scotoperiods (13:11, 15:9, and 18:6). Larvae

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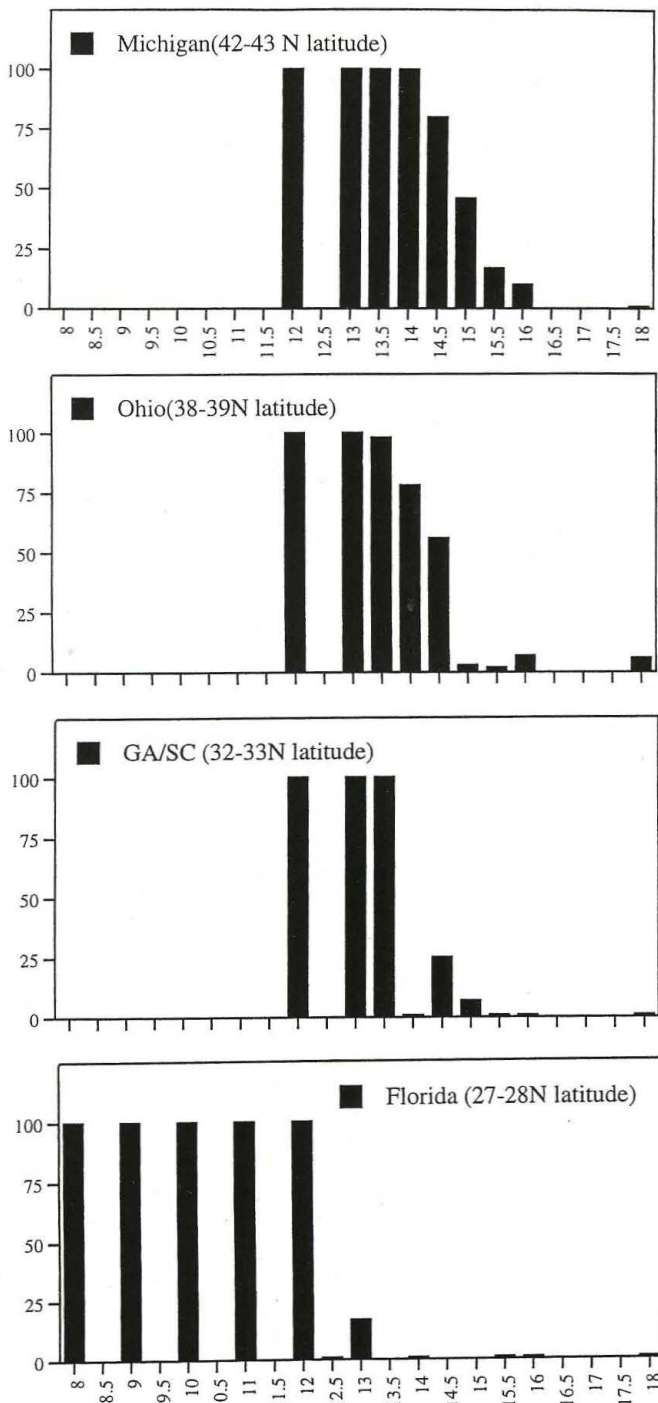


Fig. 1. The percentage of diapausing individual pupae (axis) resulting from larval rearing under various photophase durations (abscissa). Four major populations include: 1) Michigan (2 families from Ingham Co.; and 4 families from St. Joseph Co.); 2) Ohio (Lawrence and Gallia counties; 37 families); 3) South Carolina (1 family, Aiken Co.) and Georgia (2 families, Clarke Co.); and 4) Florida (1 family from Levy Co.; and 8 families from Highlands Co.). The critical inducing photoperiod (50% diapause) appears to be 14.5-15h for southern Michigan, 14-14.5h for southern Ohio, 13.5-14.0h for Georgia/South Carolina, and 12.0-12.5h for central Florida.

were reared in groups of 5 on sassafras leaves in screened petri dishes. Leaf moisture was maintained using aquapics. Fresh leaves were provided when necessary: 1-2 times per week for early instars and 2-3 times per week for later instars. Three replicates of 5 larvae per female were set up per treatment for 8 females. Larvae were set

up during July and pupated during August. The 1992 Ohio experiment was conducted at a constant 24°C under four photo:scotoperiods (13:11, 14:10, 15:9, and 18:6). Three-five replicates of 5 larvae were set up from the same group of trees in 1991. Larvae in this experiment were set up in early August and pupated during late August and September 1992.

In the 1993 Ohio experiment, larvae were set up at 2 to 3 per dish and placed in individual dishes at day 10. Each dish was randomly assigned to one of the following photo:scotoperiods: 12:12, 13.5:10.5, 14:10, 14.5:9.5, 15:9, 15.5:8.5, 16:8, 18:6, and 24:0. More than 450 larvae were set up from 8 different female lines between 10 and 16 August. Larvae were reared at 25°C and pupated during September. Also during 1993, 131 larvae were set up across the same photoperiods from 9 different Michigan female lines on 13, 14, 21 and 22 August which pupated during September.

In the 1994 Ohio experiment, five larvae were set up per dish and placed in individual dishes at 10d. More than 430 larvae were set up from 11 different female lines between 7 and 12 August. Each dish was randomly assigned to one of the following photo:scotoperiods: 12:12, 13:11, 14:10, 14.5:9.5, 15:9, 15.5:8.5, 16:8, and 18:6. Larvae were reared at 25°C and pupated during September. Also during 1994, 197 larvae were set up across the same photoperiods from 2 different Michigan female lines between 31 July and 8 August, which pupated during September. In addition, from 18 to 25 August, 60 larvae from 2 Georgia females were distributed across the same photoperiods.

In the 1995 Ohio experiment, 5 larvae were set up per dish and placed in individual dishes at day 10. A total of 300 larvae were set up from 6 different female lines between 7 and 12 August. Each dish was randomly assigned to one of the following photo:scotoperiods: 13.5:10.5, 14:10, 14.5:9.5, 15:9, and 15.5:8.5. Larvae were reared at 25°C and pupated during September. All *troilus* from New Ellentown, South Carolina were from one female and were spread evenly across the same five treatments.

All Florida larvae were reared at 25°C on red bay, their usual host, because these females were collected in March and April before sassafras leaves were available. In 1993, 456 larvae from 4 female lines were set up individually in petri dishes between 3 and 10 April. Each female's offspring were equally distributed across treatments, but assigned in random order. Nine photo:scotoperiods were used: 12:12, 13:11, 13.5:10.5, 14:10, 14.5:9.5, 15:9, 15.5:8.5, 16:8, and 18:6. The larvae pupated during May. In 1994, five larvae were set up per dish and placed in individual dishes at day 10. Five photo:scotoperiods were used: 8:16, 9:15, 10:14, 11:13, and 12:12. A total of 158 larvae from 3 female lines was set up from 7 to 10 April and pupated in May. In 1995, five photo:scotoperiods were used: 10:14, 11:13, 12:12, 12.5:11.5, and 13:11. A total of 202 larvae from 5 female lines was set up from 4 to 16 April.

For all experiments, resulting pupae were handled in the same way. Pupae were placed in individual 125mm diameter petri dishes with the lid and based separated by a 175mm high screen cylinder and returned to the chamber in which they were reared. Pupae were checked daily for emergence and kept under the same photoperiod treatment for at least six weeks. Those that did not emerge during that 6-week period were assumed to be in diapause. Pupae that do not diapause usually emerge within 3 weeks at these 24°-25°C temperatures.

RESULTS

In the 1991 Ohio experiment, all individuals developed directly and emerged when reared under a 18:6 photo:scotoperiod (Table 1). In contrast, no individuals reared under a 13:11 photoperiod emerged within the 6 weeks immediately post-pupation. These in-

Table 1. The ratio of diapausing *Papilio troilus* pupae for offspring of females from two adjacent counties in southern Ohio, to total pupae reared under various photoperiods. All larvae were reared at 25°C (24°C in 1991 and 1992). Diapause is defined here to mean any live pupa that did not emerge as an adult within the 6-week period immediately post-pupation.

Source#	Larvae#	Families	Photoperiod												
			10	11	12	12.5	13	13.5	14	14.5	15	15.5	16	18	24
Ohio															
1991	360	8	—	—	—	—	32/32	—	—	—	4/39	—	—	0/48	—
1992	320	4	—	—	—	—	10/10	—	7/7	—	0/12	—	—	2/18	—
1993	450	8	—	—	36/36	—	—	29/29	29/37	23/36	1/35	1/45	1/38	0/37	0/40
1994	430	11	—	—	39/39	—	54/54	—	—	10/36	1/41	0/50	6/59	7/49	—
1995	300	6	—	—	—	—	—	55/57	43/57	48/55	0/52	2/55	—	—	—

individuals did emerge in the following spring (1992) after they had been stored at 5°C throughout the winter. All but 4 of 39 pupae under the 15:9 treatment developed directly. The four diapausing individuals were siblings from a single Scioto County, Ohio female.

In the 1992 Ohio experiment, all individuals reared under the 15:9 photo:scotoperiod and 88.9% of 18 individuals reared under the 18:6 photoperiod developed directly and emerged as adults. No individuals reared at 14:10 or 13:11 photoperiods developed directly (Table 1).

Similarly, in 1993, 1994, and 1995 the Ohio *P. troilus* pupae reared from Lawrence and Gallia county females collected in July or August mostly diapaused after rearing at daylengths of 14.5h (100% at 12h, 100% at 13h, 98% at 13.5h, 78% at 14h, and 64% at 14.5h) or less, whereas few diapaused with longer daylength (3% = 15h, 2% = 15.5h, 7% = 16h, 6% = 18h and 0% = 24h; Fig. 1).

The threshold of photophase (daylength) for 2 populations of Michigan *P. troilus* to diapause seems to be near 15h. Complete diapause (100%) resulted from 12h, 13h, 13.5h, and 14h, with 80% at 14.5h, 46% at 15h, 17% at 15.5h, and 10% at 16h of light. No individuals diapaused at 18h and 24h photoperiods (Fig. 1).

The Georgia/South Carolina threshold appears to be less than 14.0h (0% diapause) and more than 13.5h (100% diapause; see Fig. 1). Florida spring populations appear to have a critical response for diapause induction at daylengths less than 12.5h. Complete diapause induction (100%) was observed for 8h, 9h, 10h, 11h, and 12h of photophase with no diapause observed at 12.5h (Fig. 1; and Tidwell, 1995).

DISCUSSION

The critical photoperiod for inducing diapause in most Ohio *Papilio troilus* is less than 15h of light a day but more than 14.5h. In contrast, for *P. polyxenes* Fabricius, photoperiods of 13 to 14 hours of light per day produce varying proportions of diapausing and nondiapausing pupae with more direct development at longer photoperiods (23% at 13:10, 79% at 14:10; Hazel and West, 1983).

In southern Ohio (about 39°N latitude), *P. troilus* larvae would experience 15h of daylight around 28 June, 14.5h of daylight around 23 July, and 14h around 7 August. Although decreasing daylength may be more effective in inducing diapause, larvae still growing during mid-July would receive the photoperiod cues that were effective for diapause induction in our study.

The responses to longer photoperiods observed in some families of our study are consistent with the observations of Opler and

Krizek (1984) that some pupae from each generation overwinter. Such a conservative response to environmental cues is a disadvantage when the growing season turns out to be long and favorable, but it is advantageous when the season is short and unfavorable (Taylor, 1980a, 1980b). Prolonged diapause over 2 or more years may have been selected for in northern corn rootworms, *Diabrotica barberi* Smith and Lawrence, because of crop rotation management out of corn in the midwestern part of the USA (Landis *et al.*, 1992). However, other studies with *P. troilus* suggest that temperature (not photoperiods) are most critical to diapause termination (Deering *et al.*, 2005), and we have seen very few spicebush swallowtail pupae that remain in diapause as multi-year bet hedgers.

Under standard rearing conditions and 16:8 photo:scotophase, the proportion of larvae developing directly decreased among populations of the eastern tiger swallowtail, *P. glaucus*, with increasing latitude into New York State (Hagen and Lederhouse, 1985) and from Florida to Wisconsin (Rockey *et al.*, 1987a). This variation appears to be an adaptive response to more stringent limitations on the growing season in the northern parts of the range (e.g., Tauber *et al.*, 1986; Danks, 1994). The proportion of *P. glaucus* larvae that diapaused under a 16:8 photoperiod increased later in the season, suggesting that host quality may interact with photoperiod in inducing diapause. The Ohio *P. troilus* individuals that diapaused under a 18:6 photoperiod in our 1992 study were still growing during September and it is possible this could have been partly related to the sassafras leaf quality decline in the Fall in Michigan where our experiment leaves were obtained.

In 1994, 13 Ohio individuals at 16:8 and 18:6 photoperiods also went into diapause. Once again, we are uncertain whether this result was due to family variation for "bet hedging" (9 were from two female lines; Bradford and Roff, 1993), or if host plant quality may have been the cause.

Papilio troilus is a species specialized on the Lauraceae family, and as such is geographically constrained by phytochemical ties (e.g. oviposition attractants; Frankfater and Scriber, 2003) of this ancestrally tropical host plant family (Scriber *et al.*, 1991). In temperate deciduous forests north of Florida, red bay is not available to *P. troilus*, however the northern range limits of lauraceous spicebush and sassafras host trees provide a means for extending the range and also basically defining the northern limits of the butterfly species (Scriber, 1996b).

The zone of seasonal thermal unit accumulations that regularly allows a second *P. troilus* generation basically corresponds with the northern limits of bivoltinism in *Papilio glaucus* and other Lepidop-

Table 2. The emergence of *Papilio troilus* pupae from larvae reared at each of three photo:scotoperiods. Experiments during July and August 1991.

Ohio County	Female Number	Photo:scotoperiod		
		13:11	15:9	18:6
Scioto	8283	0/2	5/5	4/4
Scioto	8285	0/4	2/6	7/7
Adams	8289	0/6	6/6	4/4
Adams	8290	0/9	10/10	13/13
Adams	8293			2/2
Adams	8294	0/5	2/2	6/6
Adams	8300	0/3	3/3	3/3
Adams	8301	0/3	7/7	9/9
Total		0/32	35/39	48/48

Table 3. The emergence of *Papilio troilus* pupae from larvae reared at each of four photo:scotoperiods. Experiments during August and September 1992.

Ohio County	Female Number	Photo:scotoperiod			
		13:11	14:10	15:9	18:6
Lawrence	9416	0/1		2/2	1/1
Lawrence	9418				2/2
Lawrence	9419	0/3	0/2	1/1	4/4
Lawrence	9505	0/6	0/5	12/12	16/18
Total		0/10	0/7	12/12	16/18

tera in the Great Lakes region of the USA (Scriber and Lederhouse, 1992). However, unlike the *P. glaucus* group, the *P. troilus* group does not have a species or subspecies that occurs north of this hybrid zone across Canada into Alaska (Scriber, 1996b), since it does not have an acceptable host plant in these areas. It is therefore not surprising that we fail to find a recessive, sex-linked obligate diapause in *P. troilus* as we do in *P. canadensis* (Scriber, 1988) and *P. eurymedon* Boisduval (West, 1995). However, as with *P. glaucus*, we have in this study observed a latitudinal cline in the critical photoperiod for diapause induction of *P. troilus* from Florida to Michigan. While some individual female variation was observed within a population, our use of multiple isofemale lines and multi-year studies provides a clear evidence of this geographic cline in *Papilio* behavior/physiology, corresponding to the environmental cue of photoperiod length. We did not examine this full range of photoperiods at different temperatures due to experimental facility limitations, however, interactions at different temperatures or thermoperiods (Beck, 1983) can alter the critical photoperiod for some insects, which allow fine-tuning to local or variable environmental conditions (Pullin, 1986; Wiklund *et al.*, 1992; Danks, 1994; Hazel, 1995; Gomi, 1997). In fact, temperature, not photoperiod, is the primary cue for diapause termination after the winter chill period (Deering *et al.*, 2005).

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