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COMPENSATORY FEEDING AND GROWTH RESPONSES OF *PAPILIO GLAUCUS* (LEPIDOPTERA: PAPILIONIDAE) LARVAE REARED IN DARKNESS.

Jennifer Muehlhaus^{1,2} and J. Mark Scriber^{1,3}

ABSTRACT

The goal was to determine the potential impact of photoperiod on feeding behavior and larval growth rates. Larvae from six different families of the eastern swallowtail butterfly, *Papilio glaucus* L. (Lepidoptera: Papilionidae) were placed into 3 different photoperiod regimes (long days at 18:6 h, short days at 12:12 h, and total darkness at 0:24 h, all at 27°C) as neonate first instars and reared to pupation. The initial 11 days reflected very slow growth of the larvae in darkness (only half the weight of the long day larvae). No differences in survival at 4 days or 11 days or until pupation were evident between any treatments. Average time to pupation (= total larval duration) was statistically identical between the treatments. However, despite their slow start during the first two instars, the larvae in complete darkness were able to increase their growth rates in the final 3 instars to such magnitude that they grew to the same final pupal size as those in the long day (and bigger than those in the short day) treatments. Such compensatory feeding and growth as a result of photoperiod has not previously been reported. Potential additional causes for such behavioral/physiological compensatory growth rates in caterpillars of other species are discussed.

INTRODUCTION

The importance of getting off to a good start can not be overemphasized with regard to subsequent success for neonate larvae of insects in general, in particular for Lepidoptera (Zalucki et al. 2002). Sometimes this can be facilitated by the butterfly mother producing larger eggs [as in Alaskan *Papilio canadensis* R & J (Lepidoptera: Papilionidae); Ayres and Scriber 1994], and placement of the eggs on the most nutritious of locally-available host plant species (especially where thermal constraints may exist; Scriber and Lederhouse 1992; Scriber 1996, 2002a; Mercader and Scriber 2005), or on young plant parts (Scriber and Slansky 1981; Scriber 1984a).

Sometimes it is also possible for the larvae themselves to "compensate" during later instar feeding for the slow initial growth during early instars. Such compensatory feeding behavior in insect larvae has been described for armyworms, *Spodoptera eridania* Stoll (Lepidoptera: Noctuidae), on hosts of low nutritional value (e.g., low nitrogen; Mattson 1980, Scriber 1984b, Slansky and Scriber 1985, Slansky 1993), low minerals or trace elements (Mattson and Scriber 1987, Fageria and Scriber 2001), or high cellulose/fiber (Peterson et al 1988, Wheeler and Slansky 1991). In addition, high allelochemical concentrations as in alfalfa (Scriber 1979, Kingsley et al. 1983), corn (Scriber 1984a, Manuwoto and Scriber 1985) and other plants (Scriber 1978) result in compensatory feeding by the southern armyworm, *S. eridania*, but such feeding compensation is not always seen for butterflies or moths (Scriber and Feeny 1979).

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Another type of stress that resulted in feeding compensation in neonate larvae of *P. canadensis* was described by Tesar and Scriber (2003). Larvae that had been exposed as eggs to cold stress (-8°C) for the longer periods (48 hours, 24 hours, 8 hours) had significantly faster neonate growth rates (0.29, 0.27, 0.24 mg/ mg.d, respectively).

Here we wanted to see the impact of darkness compared to short day 12:12 hour and long day 18:6 hour photoperiods on larval feeding behavior and growth rates of *P. glaucus* at a constant temperature of 27°C. Photoperiod effects on larval growth rates are almost unknown for insects (Slansky and Scriber 1985), and to our knowledge, nothing is known about effects on *Papilio* species. Some evidence exists suggesting that the longer photoperiod favors faster growth rates in hymenopteran sawflies, *Neodiprion swainei* Middleton (Hymenoptera: Tenthredinidae) (Philogéne and Benjamin 1971) and in banded woolly-bear caterpillars [*Pyrrharctia isabella* (J.E. Smith) (Arctiidae); Goettle and Philogéne 1978], and increased duration of *Pieris rapae* L. (Lepidoptera: Pieridae) caterpillars is potentially related to decreased ultraviolet light intensity (Thoms and Philogéne 1979).

Experimentally-restricted consumption rates have been shown to have significant impacts on the consumption and food processing efficiencies of other Lepidoptera larvae, which in turn affected growth rates (Grabstein and Scriber 1982, Tammaru et al. 2004). We therefore evaluated the potential of longer dark phases to constrain feeding behavior and to see whether non-genetic behavioral/physiological plasticity existed for these *Papilio glaucus* L. (Lepidoptera: Papilionidae) larvae.

METHODS

Field-captured females of *P. glaucus* from Nelson Co. Virginia and Clarke Co. Georgia were express-mailed to the laboratory at Michigan State University and set up in oviposition arenas to obtain offspring. Egg counts and removal as well as adult feeding with 15% honey water solution were made daily (see Scriber 1993 for details). Eggs were held at 27°C and newly hatched neonate larvae (within 1-6 hours of eclosion) were transferred using camel hair brushes to host plant leaves [tulip tree, *Liriodendron tulipifera* L. (Magnoliaceae)] and randomly allocated individually into clear plastic rearing dishes 150 mm diameter × 20 mm height. The petioles of tulip tree leaves were supported in a water-filled plastic vial with rubber cap to maintain turgor (Scriber 1977). Equal numbers of larvae (n = 8) from each of six families (= maternal lines) were allocated to Percival Growth Chambers set at 3 photoperiod treatments (18:6, 12:12, or 0:24 = light:dark; all were held at 27°C throughout the rearing period).

Initial larval weights for each family were determined by weighing groups of 4 larvae at a time (since they were so small) on a Mettler Analytical Balance (Model H80). Larvae were reared initially as neonates in groups of 4 per dish but individuals were transferred to separate dishes after a few days to avoid potential competition. Each 2 days, leaves were changed, feces were removed, and filter paper bottom liners were replaced. Weights of individuals were taken at 4 days and again at 11 days (approximately at the time when the second or third instar was completed), and at the pupal stage (3 days after pre-pupal formation). Statistical differences between treatment means (mean of families) were determined using t-tests. We did not test for family effects because the replicates were variable and low (or zero) for some indices.

RESULTS

The survival of neonates through 4 days and through 2 instars or more (at 11 days) appeared similar with the mean survival levels of the 6 families all excellent (79%- 88%) during the 4 day and 11-day period (Table 1). The weight

Table 1. Growth responses of *P. glaucus* larvae to 3 photoperiod treatments (long day 18:6h, short day 12:12h, and 0:24h = dark). Data are presented as a mean of the 6 family¹ means (\pm sd).

Treatment	(n)	SURVIVAL				WEIGHTS		
		4-day (%)	11-day (%)	to pupa (%)	days to pre-pupa	11-day (mg)	pupal (mg)	GR ² (11-p) mg/day
Long day (18:6h)								
	8	100.0	100.0	62.5	21.6	508	974	65.7
	8	87.5	87.5	87.5	23.7	245	none	-
	8	100.0	100.0	37.5	21.3	326	1162	95.4
	8	87.5	87.5	25.0	22.5	318	1039	71.4
	8	50.0	50.0	50.0	22.3	440	1283	98.9
	8	100.0	87.5	14.3	22.0	442	1402	78.5
Mean \pm sd		87.5	85.4	46.1	22.2a	380a	1172a	82.0a
		19.3	18.4	26.6	0.8	99	175	14.6
Short day (12:12h)								
	8	75.0	75.0	25.0	22.0	200	941	62.7
	8	75.0	75.0	12.5	27.0	173	593	27.5
	8	50.0	50.0	37.5	22.0	332	none	-
	8	100.0	87.5	12.5	24.0	307	883	46.1
	8	75.0	75.0	37.5	24.3	409	none	-
	8	110.0	100	25.0	23.0	347	none	-
Mean \pm sd		79.2	77.1	25.0	23.7a	295a	806 b	45.4 b
		18.8	16.6	11.2	1.9	90	186	17.6
Darkness (0:24h)								
	8	100	100	50.0	22.5	157	852	59.2
	8	87.5	87.5	62.5	23.0	232	921	54.5
	7	71.4	57.1	0	x	147	none	-
	8	75.0	75.0	50.0	22.0	179	940	68.5
	8	100	87.5	62.5	22.2	290	1041	73.1
	8	62.5	62.5	12.5	24.0	144	1065	70.6
Mean \pm sd		82.7	78.3	39.6	22.7a	192 b	964ab	65.2 ab
		15.6	16.4	26.7	0.8	58	88	7.9

The first (top) 5 families are from Virginia (Nelson Co.), females # 16262, 16268, 16273 (were dark morph), and 16283, 16284 (yellow morphs); the sixth family (# 16287) is from a yellow morph Georgia female (Clarke Co). Some pupae died after prepupal formation and before weighing. Different letters indicate significant differences between photoperiod treatment means of the family means (Tukey *t*-tests; at $P = 0.05$).

²Growth rates from day 11 to pupation.

gain at 11 days was least ($P < 0.05$) for the 0:24 (dark) photoperiod treatment (192 mg \pm 58 sd). Weight gain under the short day 12:12 photoperiod was 295 mg \pm 90 sd, and the long day 18:6 was 380 mg \pm 99 sd (but these latter two were not significantly different from each other; Table 1).

While the fast-growing larvae in the 18:6h photoperiod did have the highest mean pupal weights (mean of family means = 1172 mg \pm 175 sd), the slow growing early instars at the 0:24 (dark) treatment apparently compensated with increased growth rates in later instars and achieved mean pupal weights that were not statistically different from the long day pupae (964 mg \pm 88 sd; $P = 0.056$, t -test). The 12:12 photoperiod resulted in the smallest pupae (806 mg \pm 186 sd, mean of family means).

The mean number of days to reach the pupal stage (= total larval duration) was virtually identical in all photoperiod treatments (18:6 = 22.2 days \pm 0.8 sd, 12:12 = 23.7 days \pm 1.9 sd, and the 0:24 = 22.7 days \pm 0.8 sd for means of family means; Table 1). The growth rates from day 1 to day 11 were 34.5 mg/day; 26.8 mg/day; and 17.4 mg/day for long day, short day, and darkness, respectively. Growth rates from 11 days to pupation were 82.0 gm/day; 45.4 mg/day; and 65.2 mg/day for long, short, and dark, respectively. It is clear that the growth rates during the second half of the larval development period were about 2-fold faster in long day and 1.5-fold in short day treatments, while the growth rates of larvae in darkness increased 3.4 fold. Compensatory larval growth after day 11 is evident in darkness, with larval growth overtaking that in short days, although not significantly different than in long days (Table 1).

DISCUSSION

The slow start of neonate growth when in total darkness was not unexpected relative to the 12:12 and the 18:6 photoperiod treatments. The 11-day weights (mean of family means) in the dark (191.5 mg) were only about half that seen in the long day treatment (379.9 mg) and means in the short day treatment (12:12h) were intermediate (Table 1). While it was known that *P. glaucus* larvae do feed occasionally at night (Scriber 1975), the total darkness (except at weightings) was an unusual situation that apparently slowed their overall growth rate (neonate through the first 11 days). Although growth was slow in the dark, the survival was as good as seen for larvae in the other photoperiod treatments.

The surprising result was that these slow-growing larvae (during early larval instars) were somehow able to compensate and sufficiently increase their growth rates to achieve pupal sizes similar to those in the long day treatment. This was accomplished in the same amount of time from neonate to pre-pupa (22-23days; Table 1). The highest overall larval mortality from day 11 to day 23 occurred in the 12:12 photoperiod (75%) compared to 54 % in 18:6h and 60% in 0:24h (Table 1). Such mortality in the lab is not atypical during 3-4 week long rearing periods (Scriber, unpublished data). The reasons for the slowest growth and lowest survival in 12:12 photoperiod are not known.

These experimental bioassay results, all at a 27°C thermal regime, suggest that photoperiod alone can differentially affect the survival, growth, and fitness of *P. glaucus*. While these experimental photoperiod treatments were extreme, it has been documented here that sufficient behavioral and physiological flexibility exists to permit compensatory larval growth under such conditions. How quickly a natural field population of *P. glaucus* could adjust with genetically-based responses to photoperiod differences is not certain but rapid evolutionary responses to photoperiods have been shown for mosquitoes (Bradshaw and Holzapfel 2006).

It is known that the polyphagous species, *P. glaucus*, has adult females with extremely flexible oviposition "specificity" to permit local adjustment to

differences in abundance and/or availability (or absence) of certain local hosts. Such flexibility persists despite genetically hard-wired “rank-order” oviposition preferences that have been shown to be nearly identical, from Georgia to Michigan and west to Missouri in 7-choice oviposition assays (using plants from 7 different families; Mercader and Scriber 2005; see also Scriber 1993). It has been shown that the primary difference between *P. glaucus* and its polyphagous northern neighbor, *P. canadensis*, to be limited to a shift in host rank hierarchy due to an acceptance of *Populus tremuloides* Michaux (Salicaceae) and reduced specificity for *Liriodendron tulipifera* in *P. canadensis* (Mercader and Scriber 2007). These adult behaviors greatly impact the success of offspring since these butterfly larvae do not change host plants as many moth larvae do (Singer 2001).

Larval “compensatory responses” have also been detected in the northern *P. canadensis* where behavioral and physiological adjustments in feeding of neonates resulted in progressively faster growth in response to longer periods of experimental cold stress (8, 24, and 48 hours) encountered while they were in the egg stage (Tesar and Scriber 2003). In addition to stressful abiotic (cold) conditions and poor host plants (low nutritional value or high allelochemical concentrations; Slansky and Scriber 1985), here we add compensatory feeding by *P. glaucus* in darkness (0: 24h photoperiod).

We do not know whether the increased growth response seen here was possible because of faster consumption rates (RCRs), higher efficiencies (approximate digestibilities = ADs, efficiency of conversion of digested food = ECDs, or efficiency of conversion of ingested food = ECIs; see Scriber and Slansky 1981) or by a combination of these behavioral and physiological adjustments. It is also not clear whether such larval compensatory responses as seen here in “generalist feeders” such as these *P. glaucus* (and *P. canadensis*; Tesar and Scriber 2003; southern armyworms, Scriber 1984a,b; fall armyworms, Wheeler and Slansky 1991; and others reviewed in Slansky 1993) would be expected to occur in host specialists (Scriber 2005). Optimal diet selection does occur in insects (Waldbauer and Friedman 1991) but the physiology and behavioral mechanisms permitting compensatory feeding and growth remain largely unknown (Scriber 2002b). It is also possible that the early instars benefit relatively more from daylight (solar basking; Ayres and Scriber 1994) for growth in the field (and do poorly without it, as seen here), while larger, later instars with smaller surface to volume ratios, might be able to feed very efficiently at night (consuming some water/dew on the leaf surfaces, and also escaping from visual searching predators). In other words, darkness (or perhaps heavy shade in a forest) may not be a natural hindrance for such caterpillars, except for early instars.

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