

THERMAL REQUIREMENTS FOR POSTDIAPAUSE
DEVELOPMENT AND SURVIVAL IN THE GIANT SILKWORM,
HYALOPHORA CECROPIA (LEPIDOPTERA: SATURNIIDAE)

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Abstract.—We investigated the thermal requirements for development and survival in the giant silkworm, *Hyalophora cecropia* (L.) (Lepidoptera: Saturniidae) at 5 temperatures (L:D 16:8). The developmental times ranged from an average of 50 days at 15.6°C to 17 days at 26.7°C. Males developed slightly faster than females at all temperatures except 26.7°C. In females, the lower thermal threshold, t , and the thermal constant, K , were 10.4°C and 276 degree days (°d), respectively. In males, the respective t and K values were 9.2°C and 301 °d. The percentage mortality (pupal to adult) was very low (0 to 11%) at all temperatures. The sex ratio was approximately 1:1.

The annual life cycle of a univoltine insect species consists of a period of activity (reproduction and development), a period of dormancy (including diapause), and the intervening transitional periods (diapause induction and postdiapause development). To understand the phenology and population dynamics of univoltine insects, and to rear these species efficiently in the laboratory, it is important to understand the primary environmental factors regulating each phase.

The giant silkworm, *Hyalophora cecropia* (L.), is the largest and best-known of the North American saturniids. Much of the research on this univoltine insect has focused on its dormancy, including physiological and ecophysiological aspects of its diapause (e.g., Williams 1956, 1969; Mansingh and Smallman 1966; Sternburg and Waldbauer 1969, 1978; Waldbauer and Sternburg 1973, 1978; Willis et al. 1974; Waldbauer 1978).

Despite these important studies, a quantitative assessment of the factors controlling postdiapause development of the cecropia moth has not been made (see Waldbauer 1978). Because temperature is one of the most important abiotic factors influencing development in insects, we investigated the

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thermal requirements for postdiapause development and survival in *H. cecropia*.

Materials and Methods

We obtained ca. 70 viable eggs from a mated female caught in Ithaca, New York (Tompkins Co.). Following hatching, the larvae had access to a constant supply of cherry and black willow leaves. Initially, we placed 10 young larvae in each of 7 2-pint jars. As the larvae grew, we separated them so that there were 1 or 2 larvae per jar. In addition, we reared some of the large larvae in well-vented 12 × 12 × 6-inch plastic boxes. All of the containers were cleaned daily.

The eggs and young larvae were kept at room temperature and natural photoperiod. We maintained the older larvae at $24 \pm 1^\circ\text{C}$, L:D 10:14. After the cocoons were spun, we held them under a $24 \pm 1^\circ\text{C}$, L:D 10:14 regimen for 3½ to 4 weeks. Because no emergence occurred, we assumed that all individuals were in diapause.

Subsequently, we transferred the cocoons through a series of decreasing temperatures: 21, 18.3, 15.6, 10, and 4.4°C (all $\pm 1^\circ\text{C}$, at L:D 10:14). We maintained the cocoons for 2 weeks under each condition, except at 4.4°C , where the cocoons were held for 4 months to allow for the completion of diapause.

To determine the effect of temperature on postdiapause development, we divided the cocoons into 6 groups of about 10 each. One group was transferred to each of the following 5 temperature conditions (15.6, 18.3, 21, 24, and 26.7°C) under long days (L:D 16:8) (Table 1). The sixth group was transferred to 24°C and maintained under short days (L:D 10:14); its served as a control to show that diapause had ended.

We recorded the number of days taken for the moths to emerge in each condition. The reciprocal of the mean developmental time (1/days) was plotted against temperature and the resulting curve was tested for linearity with the ANOVA test (Snedecor and Cochran 1967). The lower theoretical threshold temperature, t , was obtained by extrapolating the linear regression of 1/days vs. temperature through the x-axis. We then calculated the thermal constant, K , by the equation $K = y(d - t)$, where y is the mean developmental time in days, and d = temperature in $^\circ\text{C}$ (Andrewartha and Birch 1954).

Results

Table 1 shows the mean developmental times for each sex of *H. cecropia* (pupal to adult stages) at 5 constant temperatures. The number of days to emergence ranged from 15–20 days at 26.7°C to 38–62 days at 15.6°C . At all temperatures except 26.7°C , females took slightly longer to emerge than

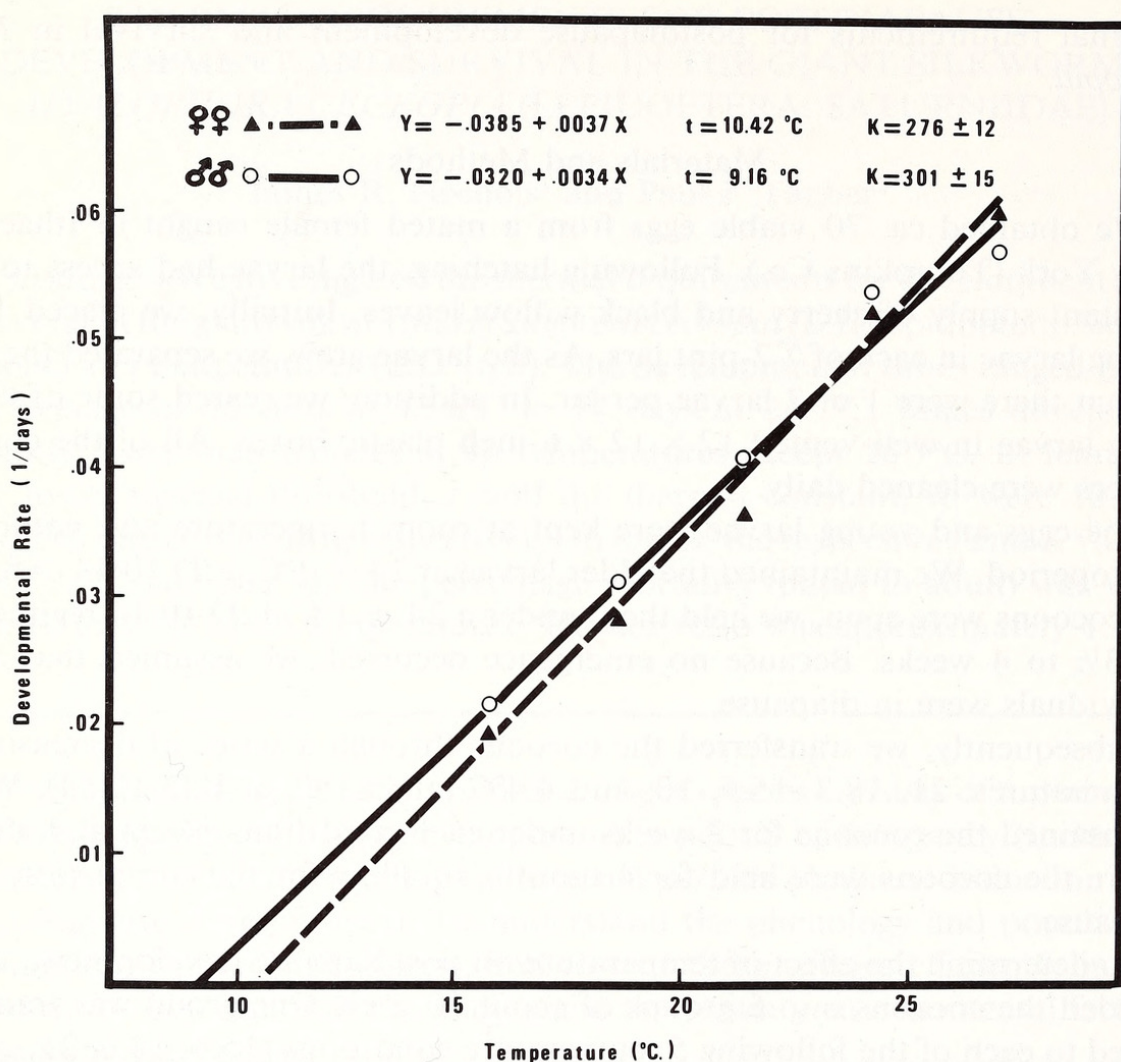


Fig. 1. Postdiapause developmental rates for the pupal to adult stages of *Hyalophora cecropia* at constant temperatures.

males, but the difference was only significant at 21°C (t-test, $P < 0.05$) (Table 1). The distribution of emergence was continuous for both females and males at each temperature except 15.6°C, where adults emerged more slowly and sporadically.

The lower theoretical threshold, t , is 10.4°C for females and 9.2°C for males (Fig. 1). The thermal constant, $K \pm \text{SD}$, is 276 ± 12 and 301 ± 15 degree days (°d) above t for females and males, respectively. Development varied linearly with temperature between 15.6°C and 26.7°C ($P < 0.05$).

The overall sex ratio (all temperatures combined) was 57% females and 43% males. This ratio—calculated from a total of 56 including 4 unemerged animals that were dissected after death—did not differ significantly (chi-square test, $P < 0.05$) from a 1:1 ratio.

The percentage mortality of pupae and pharate adults was very low at all temperatures. However, at 26.7°C, approximately half of the emerged moths failed to expand their wings fully (Table 1).

Table 1. Postdiapause developmental rates, mortality, and sex ratio of *H. cecropia* at various constant temperatures. Females: $t = 10.4^{\circ}\text{C}$; $K = 276^{\circ}\text{d}$. Males: $t = 9.2^{\circ}\text{C}$; $K = 301^{\circ}\text{d}$.

Temp. ($\pm 1^{\circ}\text{C}$)	% mortality	Developmental time (days)			Sex ratio (%)	
		♀ ♀	♂ ♂	Combined	♀	♂
26.7	10 (10)*	$17 \pm 2.0^{**}$ (5)	17.8 ± 2.1 (4)	17.3 ± 1.9 (9)	55	45
24.0	0 (8)	19.2 ± 1.3 (5)	18.7 ± 0.6 (3)	19.0 ± 1.1 (8)	62	38
21.1	0 (10)	27.6 ± 1.4 (7)	24.7 ± 1.2 (3)	26.7 ± 1.9 (10)	70	30
18.3	0 (10)	35.2 ± 2.3 (5)	33.8 ± 3.1 (5)	34.5 ± 2.7 (10)	50	50
15.6	11 (9)	52.3 ± 8.4 (3)	48.6 ± 7.2 (5)	50.0 ± 7.3 (8)	44	56

* (No.) = number tested.

** $\bar{x} \pm \text{SD}$.

Developmental rates of females and males under L:D 10:14 (24°C) were not significantly different from those under L:D 16:8 (24°C) (t-test, $P < 0.05$).

Discussion

Development and temperature.—Sternburg and Waldbauer (1969) observed that *H. cecropia* males emerge earlier than females under natural conditions. Our preliminary results (Fig. 1) suggest that the earlier emergence of males can be explained by differences in thermal requirements for the postdiapause development of the 2 sexes. That is, males begin development at a lower threshold temperature than females. In addition, males have a slightly faster rate of development than females at all but the highest temperature tested (Table 1).

The lower theoretical threshold temperature (t) for development and emergence was ca. 10°C. This is consistent with Williams' (1956) observation that some morphological development, but not emergence, occurred in *H. cecropia* at 6°C.

Emergence pattern and sex ratio.—Sternburg and Waldbauer (1969) and Waldbauer and Sternburg (1978) observed a distinct bimodal emergence pattern in field populations of *H. cecropia* in Illinois (i.e., emergence in the 2 broods was separated by ca. 1 month). They attributed the bimodality to variation in diapause termination, not to variation in rates of development after diapause had ended. In our experiments, emergence did not exhibit bimodality, but was unimodal at all temperatures. We suggest that the prolonged period of chilling experienced by our experimental animals allowed

diapause to terminate in all individuals before transfer to warmer conditions and thus masked the expression of any variation in diapause termination that might have been present.

Our sex ratio data and photoperiodic tests are consistent with this hypothesis. Sternburg and Waldbauer (1969) found that 65% of their early-emerging brood and 43% of their late-emerging brood were females; whereas 57% of our adults were females (Table 1). This intermediate sex ratio suggests that if there were two broods in our population, both emerged simultaneously. Similarly, developmental rates were not affected by photoperiod (L:D 16:8 and L:D 10:14), indicating that diapause had terminated in all individuals before removal from cold conditions. Thus, our results are consistent with Waldbauer and Sternburg's conclusion that bimodality in *H. cecropia* emergence is the result of variation in diapause termination, rather than post-diapause development.

The unimodal emergence pattern in our experiments may also have resulted from limited genetic variability. That is, natural *H. cecropia* populations from Ithaca, New York, may not have the genetic variability that produces bimodal termination. It is also possible that our experimental population, which was derived from limited stock, did not harbor the full range of variability. Thus, additional studies are needed to establish the relative roles of environmental and genetic factors in determining emergence patterns in *H. cecropia* populations in central New York.

Mortality.—The percentage mortality of immatures within cocoons was low (~4%) and, apparently, unrelated to temperature over the range of temperatures we used (Table 1). However, at our highest temperature (26.7°C), almost half of the adults failed to expand their wings fully and died shortly after emergence. This mortality can be attributed to desiccation during emergence; *H. cecropia* emerges early in the day (Truman 1972) when daily temperatures are low and relative humidity is high. Therefore, we conclude that *H. cecropia* should be reared at temperatures around 24°C for relatively fast development and high rates of survival.

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