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Effect of Light Intensity on the Time of Egg Hatch in *Metrioptera hime* FURUKAWA (Orthoptera:Tettigoniidae)

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Abstract When eggs of *Metrioptera hime* were kept under daily cycles of change in light intensity, they mainly hatched within 2 h after the rise of light intensity. When eggs were exposed to a single signal of lowering light intensity, they hatched around 12–14 h after the signal provided that the drop in light intensity was large. A single signal of increase in light intensity also triggered hatching. When eggs were exposed to various light intensities (400, 100, 10 and 1 lux) under a thermoperiod (25 : 15°C, each 12 h), eggs hatched during the low temperature phase. However, the lower the light intensity, the later the time of hatching after the temperature fall. The same result was observed with a single signal of temperature fall.

Key words: time measuring mechanism; long-horned grasshopper; photoperiod; thermoperiod; light intensity.

Introduction

In *Metrioptera hime* the daily hatching time was determined by photoperiod or thermoperiod, and the signals of light-on, light-off, temperature rise and fall are involved in the time measurement for hatching (ARAI, 1977, 1979a, b). In the previous experiments leading to the above conclusion, a light period (about 400 lux) was alternated with a dark period (0 lux). In some insects, a change in light intensity affects the timing of various activities (ENGELMANN, 1966; CHANDRASHEKARAN and LOHER, 1969; SOWER *et al.*, 1970). I examined whether increase or decrease in light intensity has the same effect on the timing of egg hatch in *M. hime* as light-on or light-off. I obtained positive results and determined the effective range of the shift in light intensity. A temperature cycle also determines the time of hatching and the presence of light affects this timing (ARAI, 1979a). Therefore, I subjected eggs to temperature cycles or a single temperature fall under various intensities of illumination for further understanding of such an influence of light on the time measurement.

Materials and Methods

Eggs for experiments were laid by adults collected at Hirosaki in July, 1972–1995. The methods of rearing adults, collecting and storage of eggs,

Light intensity		No. of hatching											Hatchability (%)	
Low (lux)	High (lux)	Low light intensity or darkness					High light intensity							
100	400	2	5	4	1	4	6	8	3	2	1	2	5	53.8
10					3	3	7	19	9		3		4	60.0
1			2				1	40	5				1	61.3
0								57	2					73.8
10	100		4		4	3	4	9	5	3	2	1	1	46.3
1			1	1	2	2	4	18	3	2	4	2		48.8
0							3	53	2					72.5
1	10		2	2	5	2	4	3	4	1	9	7	1	51.3
0							5	49	5					75.00
0	1						5	52	1	2				76.25
		0					6	12		18		24		HR
		T I M E												

Fig. 1. Effects of light intensity cycles on hatching time and hatchability of *M. hime* at 15°C. Each treatment comprised of 80 eggs. The total numbers of egg hatching every 2 h is shown over the whole period of observation.

observations of hatching and the regulation of temperature conditions were the same as described previously (ARAI, 1977). The light intensities used in experiments were 400, 100, 10, 1 and 0 lux as measured by a high sensitive photometer (Shimazu Co., Tokyo). The light source was a 10w daylight fluorescent tube, and the light intensity was controlled by covering Petri dishes containing eggs with tracing and/or filter paper. For permanent dark, dishes were covered with black flockpaper. For observations during the dark period, dim red light was used for about 10 seconds. Observations under 100, 10 and 1 lux were made without changing the light intensity.

Results

1. Effect of light intensity cycle

Under 12L : 12D hatching peak usually appears within 2 h after light-on and a few eggs hatch before light-on (ARAI, 1977). Then the hatching pattern was observed under square wave cycles of low and high light intensities each

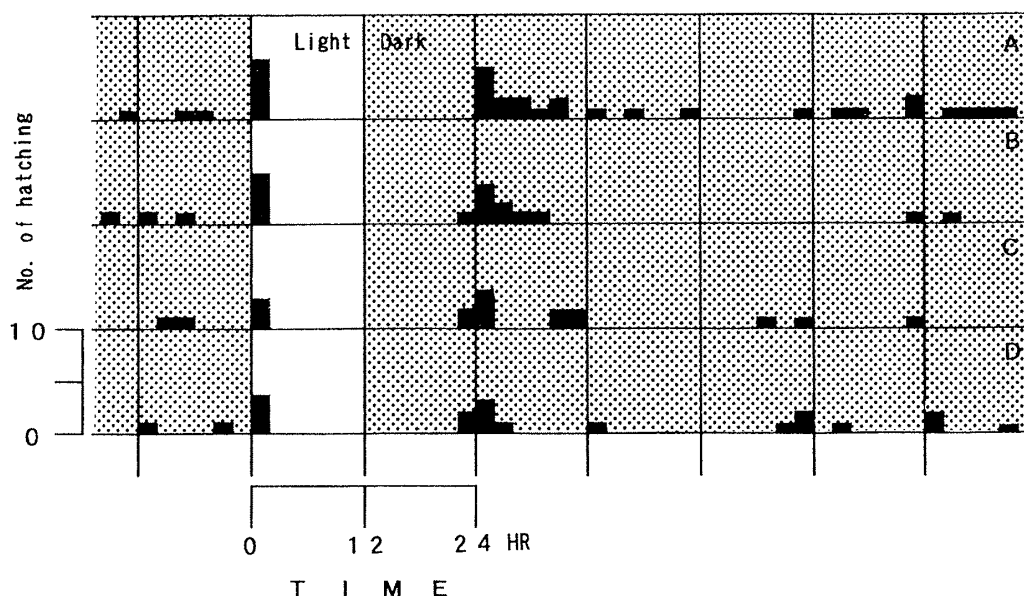


Fig. 2. Effects of 12 h-light pulse of various light intensities in otherwise continuous darkness on hatching time of *M. hime* at 15°C. Each treatment comprised of 150 eggs. Light pulses are 400 lux (A), 100 lux (B), 10 lux (C), 1 lux(D).

lasting for 12 h. When the low light intensity was 100 lux and the high one was 400 lux (indicated as L100 : H400), the eggs hatched more or less irregularly (Fig. 1). The hatching larvae concentrated around the rise of light intensity under L10 : H400 and most eggs hatched within 2 h after the rise of light intensity under L1 : H400. The concentration of egg hatching was not observed under L10 : H100 and L1 : H10. When eggs were exposed to L1 : H100, hatching occurred not only within 2h after the rise of light intensity but also before and after the light increase. When one component of the cycle was 0 lux, that is, a light period alternated with a dark period, most eggs hatched in 2 h after light-on, even with the photophase was only 1 lux.

The hatchability was higher than 70% in the cycles of light and dark, but about 45–60% in the cycles of low and high intensities. The cycles of high and low light intensities thus decreased not only the accuracy of timing but also the hatchability. However, if the difference in light intensity between the two periods was large enough (e.g. L1 : H400), the effect on hatching time was similar to that of a normal photoperiod. Even light of 1 lux was effective to synchronize hatching when combined with darkness.

2. Effects of light pulse of various light intensities and decrease in light intensity

When a single 12 h light pulse was given in otherwise dark conditions, hatching peaks were observed within 2 h after light-on and around 12–14 h after light-off (Fig. 2). Since light pulse of 1, 10 and 100 lux gave similar results,

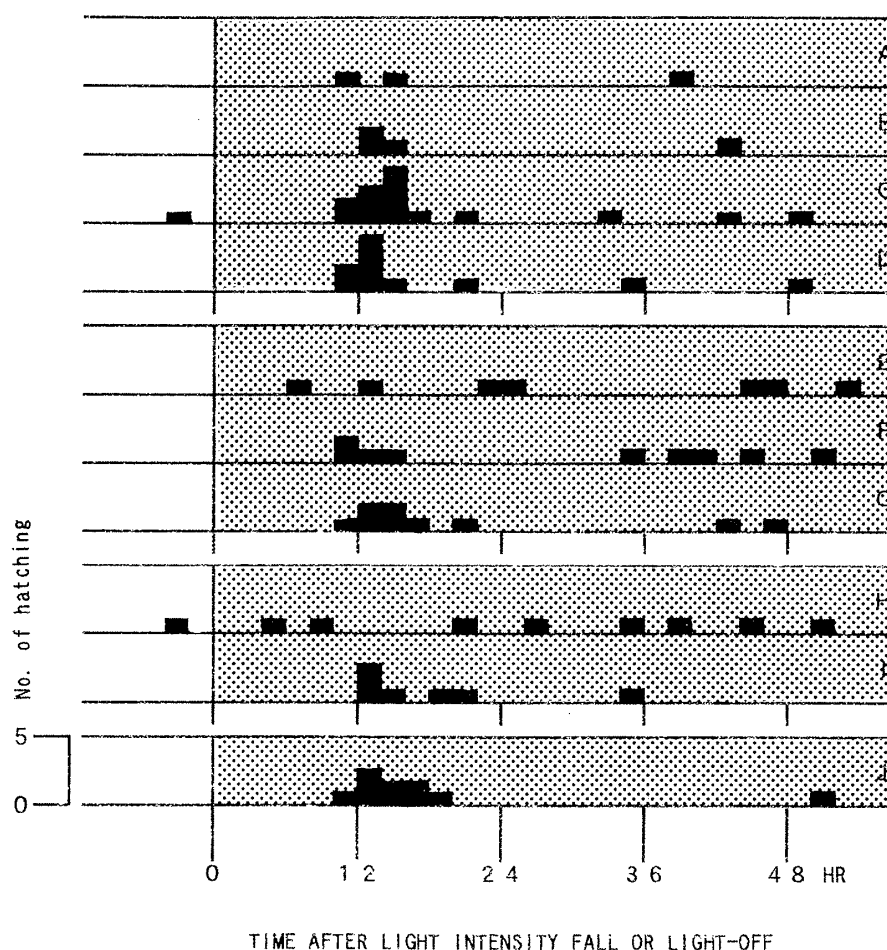


Fig. 3. Effects of light intensity drop and light-off step on hatching time of *M. hime* at 15°C. Each treatment comprised of 100 eggs.

A: 400→100 lux. B: 400→10 lux. C: 400→1 lux. D: 400→0 lux. E: 100→10 lux. F: 100→1 lux. G: 100→0 lux. H: 10→1 lux. I: 10→0 lux. J: 1→0 lux.

hatching reaction was triggered by light-on if the light exceeded the threshold lower than 1 lux. Thus, light-on directly invokes hatching and light-off is taken as a signal to start the time-measurement for hatching 12–14 h later.

In the next series I examined whether a drop in light intensity could be as effective as light-off in determining the hatching time or not. A hatching peak was observed about 12–14 h after drops from 400 lux to 10 or 1 lux (Fig. 3B, C), and also from 100 to 1 lux (Fig. 3F), but not after drops from 400 to 100 lux (Fig. 3A), from 100 to 10 lux (Fig. 3E) and from 10 to 1 lux (Fig. 3H). In the transfers to darkness, peaks occurred about 12–14 h after light-off irrespective of the preceding intensity of light (Fig. 3D, G, I, J). These results indicate that if the decrease in light intensity surpasses a certain amount, it serves as a signal for the timing of hatch similar to light-off. Also, light-off is quite effective, even when the preceding light intensity was 1 lux.

Light intensity (lux)	No. of hatching										Hatchability (%)	Mean time of hatching $\pm$ S.D. (h)
	Cool phase (15 $^{\circ}$ C)					Warm phase (25 $^{\circ}$ C)						
400	12	55	48	17	1						83.1	6.1 $\pm$ 1.71
100	8	53	56	16	3	2					86.3	6.4 $\pm$ 1.86
10		32	50	35	11	3					81.9	7.5 $\pm$ 1.99
1	1	24	46	41	15	4					81.9	7.9 $\pm$ 2.07
0			3	20	43	70	2				86.3	11.7 $\pm$ 1.64
	0	6	12	18	24	30	36	42	48	54		
	T I M E											

Fig. 4. Effects of thermoperiod (25 : 15°C, each 12 h) under various light intensities on hatching time and hatchability of *M. hime*. Each treatment comprised of 160 eggs. The total number of eggs hatching every 2 h is shown over the whole period of observation.

3. Effects of light intensity under thermoperiod or single signal of temperature fall

The timing of hatching in *M. hime* can be determined by a temperature cycle or fall as well as similar light regimes. The effect of temperature regimes on the timing of hatching peak is modified by light conditions (ARAI, 1977). In the present study, this modifying effect of light on temperature signals was analyzed further by changing the light intensity.

In a temperature cycle under continuous darkness, more than 50% of the eggs hatched within 2 h after the temperature rise (Fig. 4). Under 400 and 100 lux, about 80% hatched 4–8 h after the temperature decrease with an average time of about 6 h (not significantly different, $P > 0.05$, U-Test). The hatching peak occurred about 7–8 h after temperature drop under 1 lux and 10 lux (not significantly different, $P > 0.05$, U-Test) indicating that hatching was somewhat delayed as the light intensity decreased. Similar results were obtained when a single temperature fall was provided; the hatching peak occurred about 5 h after temperature fall under 400 and 100 lux (not significantly different, $P > 0.05$, U-Test) but later as the light intensity decreased although the differences were statistically significant ($P > 0.05$, U-Test) (Fig. 5). Thus, the timing of hatching initiated by a temperature signal is affected by the presence of light and also by

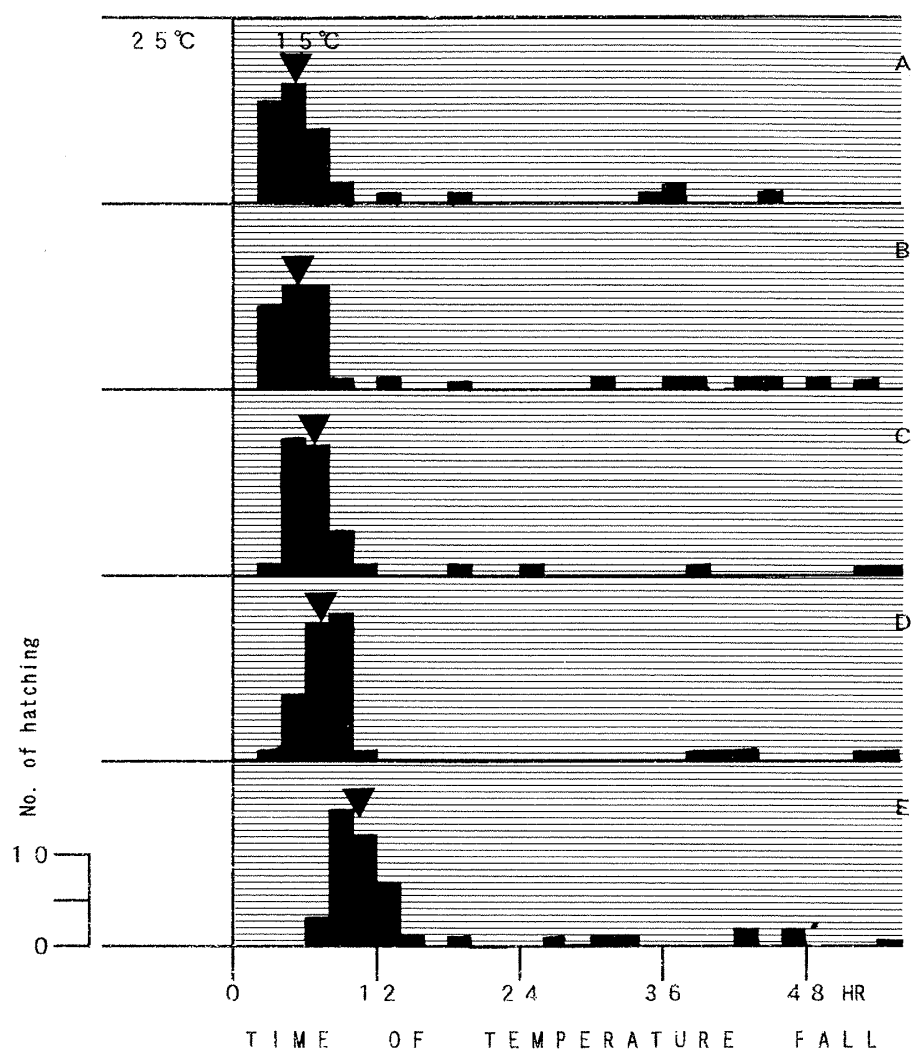


Fig. 5. Effects of temperature-fall step ($25^{\circ}\text{C} \rightarrow 15^{\circ}\text{C}$) under various light intensities on hatching time of *M. hime*. Each treatment comprised of 160 eggs.

A: 400 lux. B: 100 lux. C: 10 lux. D: 1 lux. E: 0 lux. ▼: mean time of hatch.

light intensity.

Discussion

1. Similarity between light-intensity changes and light-dark changes

In almost all experiments with light cycles carried out previously, a light period was combined with a dark period (0 lux). A light intensity of 1 lux was thought to be effective in forming a light period. In *M. hime*, even when the dark period was 0 lux and the light period was only 1 lux, the hatching peak came within 2 h of light-on. If the light intensity was 1 lux or more, it could be taken as a light period. Under cyclical conditions with alternating periods of

high and low light intensities with a large difference (e.g. 400 and 1 lux), a clear hatching peak was observed within 2 h of the level up. Thus, both light-on and increase in light intensity serve the same function for timing the egg hatch.

An effective signal is also provided by lowering the light intensity, if the change involved exceeds a certain level. It induces hatching mainly 14 h later. This suggests that the time measuring response initiated by a light-intensity drop and that invoked by a light-off signal are one and the same. In *M. hime*, the progression of time measuring response initiated by a light-intensity drop is not influenced by the light intensity itself. Some species of insects might perceive the photoperiod through relative changes in light intensity as indicated by the asymmetric time measurement in the photoperiodic response of *Hyphantria cunea* (TAKEDA & MASAKI, 1979) and by the photoperiodic reaction of *Acronycta rumicis* under the light intensity cycles (DANILEVSKII, 1965). The response to a change in light intensity is important for further analysis of the nature of the time-measuring system sensitive to light signal.

2. Effects of light intensity on time measurement triggered by temperature signal

In *M. hime*, the progression of time measurement triggered by a temperature signal is influenced by light (ARAI, 1977). Only a few examples to illustrate such an influence have been known: adult eclosion in *Drosophila pseudoobscura* (BRUCE, 1960), egg hatching in *Gampsocleis buergeri* (ARAI, 1979b) and *Chizuella bonneti* (ARAI, unpublished). The time of hatching may be affected not only by light itself, but also by a change in light intensity. Hatching occurred at about the same time under 100 and 400 lux, but under low light intensities of 1 and 10 lux, the hatching peaks were delayed and intermediate between those in 100 lux and DD. This delay in hatching time may be due to the decreased rates of time measuring process initiated by the temperature signal under the low light intensities.

Although the progression of the time measurement was influenced by light intensity when initiated by a temperature signal, but not when initiated by a light drop signal. Are there different time-measuring systems triggered by light and temperature signals, respectively, or does the same system change its sensitivity to light depending on the triggering signal? This is an important point to characterize the unique hourglass hatching timer in *M. hime*.

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