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ORIGINA ARTICLE：

# Photoperiod and thermoperiod to regulate egg hatching of the short-winged katydid, *Chizuella bonneti* Bolivar (Orthoptera: Tettigoniidae)

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## Abstract

The hatchability of the short-winged katydid, *Chizuella bonneti* (Furukawa, 1950) (Orthoptera: Tettigoniidae) was affected by temperature and photoperiod. It was low at 25ºC and 20ºC in continuous darkness (DD) and constant light (LL), but it increased under LD 12: 12 at 20ºC and 15ºC. The hatchability also increased under thermoperiod (25ºC: 15ºC). The egg hatching was irregular under DD and LL but it occurred in synchronization with photoperiod and thermoperiod. Hatching occurred within 2 h after light-on (L-on) under LD 12: 12 at 25ºC and 20ºC, and under LD 6: 18, 12: 12, and 18: 6 at 15ºC. The effect of the thermoperiod on hatching was also investigated where 25ºC was the warm phase (W) and 15ºC the cool phase (C) conditions both under DD and LL. Under a thermoperiod of WC 6: 18 in DD, hatching peaked within 2 h after the temperature-rise (T-rise) and around 12 h after the temperature-fall (T-fall). Hatching peaked before and after the T-rise under WC 12: 12 and within 2 h after the T-rise under WC 18: 6. In LL, hatching peaked around 8 h and around 6 h after T-fall under WC 6: 18 and 12: 12, respectively, and before and after the T-rise under WC 18: 6. In order to investigate of circadian rhythm in determining hatching time, eggs were transferred from photoperiod or thermoperiod to constant conditions. Hatching occurred in synchronization with photoperiod and thermoperiod but when eggs were transferred to constant conditions, the daily rhythm of hatching disappeared immediately. However, when eggs were transferred to constant conditions, hatching was suppressed for certain periods, suggesting the involvement of an endogenous rhythm triggered by photoperiod or thermoperiod. Hatching time was determined by a single signal of T-fall, but the involvement of a single signal of L-off was not clear. Hatching behavior was triggered by a single signal of L-on or T-rise.

**Key words**: *Chizuella bonneti*, hatchability, haiching behavior, hatching time, photoperiod, thermoperiod

## INTRODUCTION

Many insect species synchronize their behavioral activities with environmental conditions in response to varying photoperiods and thermoperiods (Saunders 2002). The timing of hatching is in most cases controlled by photoperiodic and thermoperiodic signals, for example, hatching occurs in the first half of the photophase in the walking sticks (Kalmus 1938), the stink bug, *Cardiaspina densitexta* (White 1968), and the falsemelon beetle, *Atrachya manetriesi* (Arai 1987), during dark periods in the mosquito, *Mansonia titillans* (Nayar *et al.* 1973), throughout the light period in the large backswimmers, *Notonecta triguttata* (Arai *et al.* 1994), during the photophase or cool-phase in the american grasshopper, *Schistocerca gregaria* (Tanaka 2015a, b), and during the dark-phase or warm-phase in the asiatic migratory locust, *Locusta migratoria,* (Tanaka 2015a, b). The hatching peak occurs around dawn in many species (Edward 1964; Minis & Pittendrigh 1968; Riddiford & Johnson 1971; Arai 1977a, 1979c, 1998a, b). In some species, the cucumber looper, Anadevidia peponis (Sasaki 1975), the oriental fruit fly, *Bactrocera dorsalis* (Arai, 1975), and *Gryllodes supplicans* (Arai, 1998a), hatching did not synchronize with photoperiod or thermoperiod, and occurred irregularly regardless of the time of day.

When eggs are transferred from cyclical to constant conditions, a circadian hatching rhythm persisted (Tanaka

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1961; Minis & Pittendrigh 1968; Tomioka *et al.* 1991). In the two Japanese katidids, *Eobiana engelhardti subtropica* (=*Metrioptera hime*) (Arai 1977a, 1979a, b, 1997) and *Gampsocleis buergeri* (Arai 1979c), hatching is synchronized with environmental cycles, but the hatching rhythm did not free-ran. In the northern rice katydid, *Homorocoryphus jezoensis* (Arai 1998b), the circadian rhythm of hatching persisted for several days when eggs were transferred from photoperiodic or thermoperiodic conditions to constant conditions.

The objective of this study was to investigate the effects of light and temperature signals on the hatching rhythm in *Chizuella bonneti.*

## MATERIALS AND METHODS

Eggs were obtained in the laboratory at Hirosaki University and Ashiya University from adults of *C. bonneti* collected in Hirosaki City and Owani Town (N 40.5°, E 140.5°), Aomori Prefecture, Japan, in August 1974−1995. These eggs were entered diapause. Therefore, to terminate diapause, eggs were first kept at 25ºC for 8 weeks and then at 7.0−7.5ºC for 18 weeks under continuous darkness (DD). The eggs were placed on wet filter papers on Petri dishes. In the experiments, the temperature was set with incubators (Nihon-Ikakikai K.K. and Mitsubishi K.K.) and the light source was a 10W daylight fluorescent tube.

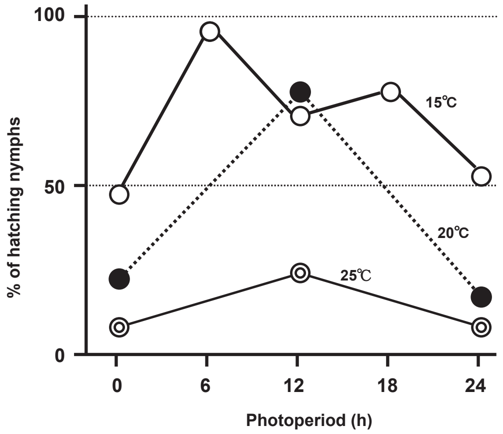

Figure 1 Effects of photoperiod on hatchability of *Chizuella bonneti* at 25ºC, 20ºC, and 15ºC after chilling for diapause completion. Each treatment comprised 100 eggs.

Hatching time was examined under photoperiods or thermoperiods and a single signal of light or temperature. Free-running rhythms were observed to confirm the circadian rhythm under constant conditions after the entrainment by photoperiods or thermoperiods.

The number of hatchings was counted every 2 h and observations were made during the dark period under dim red light (Kenko Optical Filter SR64) within 5 seconds. The dim red light did not influence the determination of hatching time.

## RESULTS

Hatchability depended on temperature and photoperiods. It was low at 25ºC, that is, 11% under DD, 7% under continuous light (LL), and 25% under 12 h light: 12 h dark photoperiod (LD 12: 12) (Fig. 1). At 20ºC, it was 73% under LD 12: 12 but it was 21 and 13% under DD and LL, respectively. At 15ºC, it was 48, 90, 67, 74, and 52% under LD 0: 24 (DD), 6: 18, 12: 12, 18: 6, and 24: 0 (LL), respectively.

Under DD and LL at 25ºC, 20ºC, and 15ºC, hatching was irregular for 5 to 15 days at 25ºC, 6 to15 days at 20ºC, and 11 to 25 days at 15ºC after the low temperature treatment (Fig. 2, 3). However, when eggs were exposed to photoperiods, they were synchronized to the photoperiods. At 25ºC, 20ºC, and 15ºC, hatching occurred within 2 h after L-on (Fig. 2, 3). Mean time and standard deviation (SD) of hatching after L-on was 0.9 h ± 1.6 h at 25ºC (Fig. 2A) and 1.0 h ± 0.3 h at 20ºC (Fig. 2B). At 15ºC, it was 1.0 h ± 0.2 h, 1.0 h ± 0 h, and 1.1 h ± 0.3 h under LD 6: 18, 12: 12, and 18: 6, respectively (Fig. 3).

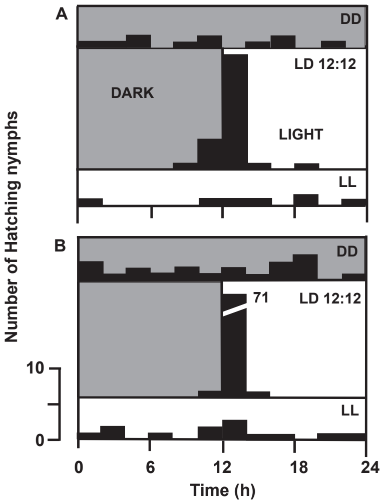

Figure 2 Effects of photoperiod on hatching time of *Chizuella bonneti* at 25ºC (A) and 20ºC (B). Each treatment comprised 100 eggs.

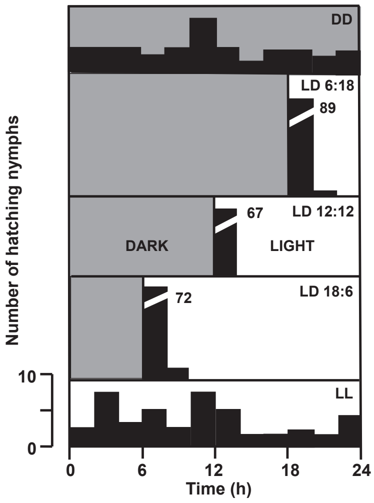

Figure 3 Effects of photoperiod on hatching time of *Chizuella bonneti* at 15ºC. Each treatment comprised 100 eggs.

Hatchability was low under constant temperature in DD and LL, but increased under thermoperiods (25℃: 15℃). Under DD, they were 62, 78, and 66% under WC 6: 18, 12: 12, and 18: 6, respectively, and 62, 84, and 54% under LL. Hatching was synchronized to the thermoperiods of warm phase (25℃) and cool phase (15℃) and continued for 5 to 18 days. In DD, two hatching peaks occurred around 6 h after temperature fall (T-fall) and within 2 h after temperature rise (T-rise) under 6 h warm phase: 18 h cool phase thermoperiod (WC 6: 18) (Fig. 4A). One of the mean time and SD of hatching after T-fall was 11.7 h ± 1.8 h and the other was 19.1 h (1.1 h after T-rise) ± 0.6 h under WC 6: 18. Under WC 12: 12 and 18: 6, hatching occurred around T-rise and within 2 h after T-rise, respectively (Fig. 4B, C). It was observed 12.2 h (0.2 h after T-rise) ± 1.2 h and 7.2 h (1.2 h after T-rise) ± 0.6 h under WC 12: 12 and 18: 6, respectively. In LL, it was 7.4 h ± 1.9 h, 5.3 h ± 2.6 h, and 5.3 h ± 2.2 after T-fall under WC 6: 18, 12: 12, and 18: 6, respectively (Fig. 5).

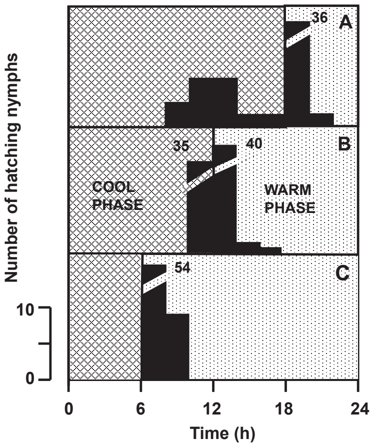

Figure 4 Effects of thermoperiod (25°C: 15°C) on hatching time of *Chizuella bonneti* under DD. A: 6-h warm-phase: 18-h cool-phase (WC 6: 18). B: WC 12: 12. C: WC 18: 6. Each treatment comprised 100 eggs.

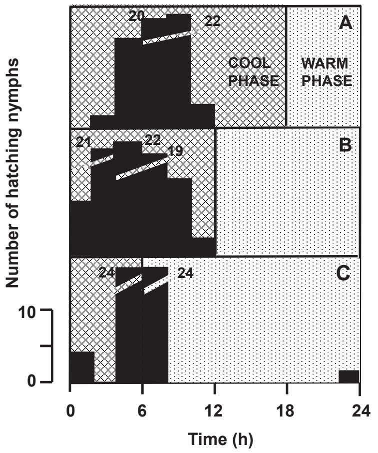

Figure 5 Effects of thermoperiod (25°C: 15°C) on hatching time of *Chizuella bonneti* under LL. A: 6-h warm-phase: 18-h cool-phase (WC 6: 18). B: WC 12: 12. C: 18: 6. Each treatment comprised 100 eggs.

In order to investigate the involvement of circadian rhythm in determining hatching time, eggs were transferred from photoperiod to DD or LL at 15℃ and the free-running rhythm was observed. Under LD 12: 12, hatching occurred within 2 h after L-on, with a precise 24 h interval (Fig. 6A). When the eggs were transferred to DD or LL after 18 cycles of entrainment under LD 12: 12, hatching did not occurred almost for more than 56 h and then hatched irregularly (Fig. 6B, C, D, E).

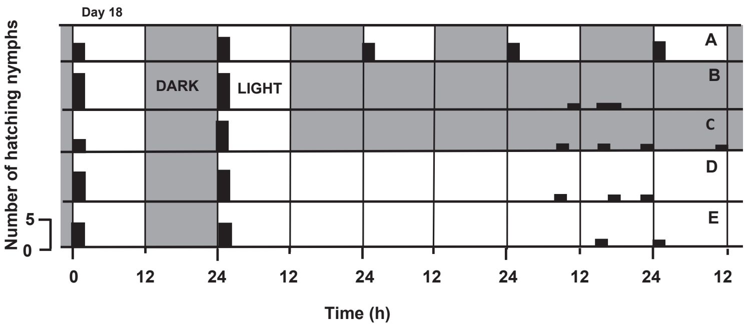

Figure 6 Persistence of egg hatching rhythm in transition from LD 12: 12 to DD or LL at 15°C of *Chizuella bonneti*. A: LD 12: 12. B, C: transfer from LD 12: 12 to DD. D, E: transfer from L! 12: 12 to LL. Each treatment comprised 120 eggs.

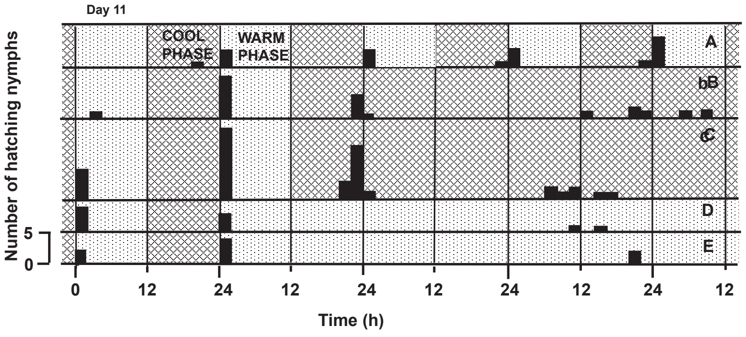

Figure 7 Persistence of egg hatching rhythm in transition from thermoperiod (25°C: 15°C, each 12 h) to constant temperatures (25°C or 15°C) under DD of *Chizuella bonneti*. A: WC 12: 12. B, C: transfer from WC 12: 12 to constant temperature 15°C. D, E: transfer WC 12: 12 to constant temperature of 25°C. Each treatment comprised 180 eggs.

When eggs were transferred from thermoperiod to constant temperature at 15℃ or 25℃ and the free-running rhythm was observed. In DD, hatching concentrated within 2 h after T-rise under WC 12: 12, with a precise 24 h cycle (Fig. 7A). When eggs were transferred to a constant temperature 15℃ after 11 cycles of WC 12: 12, the mean time and SD of hatching was 10.9 h ± 1.1 h after transferring to 15℃, and the daily rhythm of hatching disappeared (Fig. 7B, C). After the last hatching peak, hatching suppression period followed for more 30 h, and then hatching occurred irregularly. When eggs were transferred to 25℃ constant, the hatching rhythm disappeared immediately (Fig. 7D, E). Hatching suppression lasted for more 60 h, and most eggs died with a few hatched. In LL, hatching concentrated around 6 h after T-fall under WC 12: 12, with a precise 24 h cycle (Fig. 8A). When eggs were transferred to a constant temperature 15℃ after 10 cycles of WC 12: 12, the mean time and SD of hatching

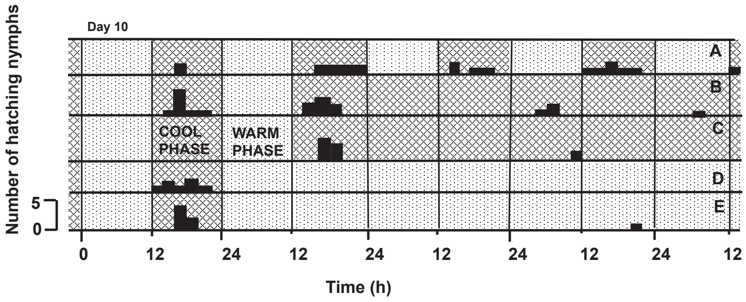

Figure 8 Persistence of egg hatching rhythm in transition from thermoperiod (25°C: 15°C) to constant temperature (25°C or 15°C) under LL of *Chizuella bonneti*. A: WC 12: 12. B, C: transfer from WC 12: 12 to constant temperature of 15°C. D, E: transfer from WC 12: 12 to constant temperature of 25°C. Each treatment comprised 180 eggs.

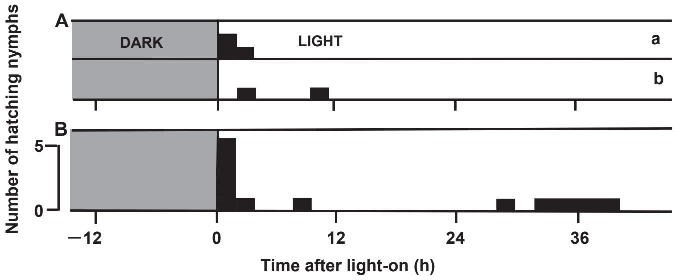

Figure 9 Effects of a single signal of L-on on the timing of egg hatching at 25°C (A) and 15°C (B) of *Chizuella bonneti*. Each treatment comprised 300eggs.

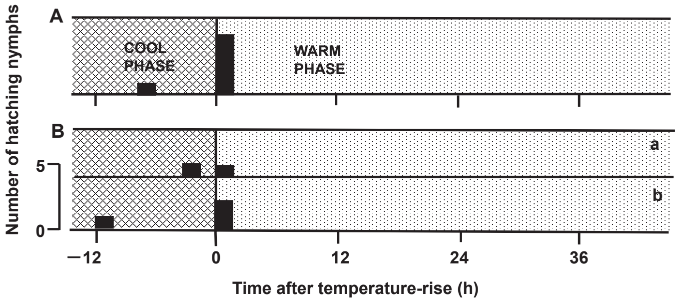

Figure 10 Effects of a single signal of T-rise (from 15°C to 25°C) on the timing of egg hatching under DD (A) and LL (B) of *Chizuella bonneti*. Each treatment comprised 300 eggs.

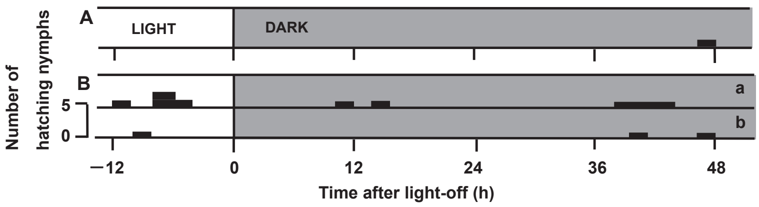

Figure 11 Effects of a single signal of L-off at 25°C (A) and 15°C (B) on the timing of egg hatching of *Chizuella bonneti*. Each treatment comprised 300 eggs.

was 5.3 h ± 1.4 h after transferring to 15ºC, and the daily rhythm of hatching disappeared (Fig. 8B, C). After the last hatching peak, hatching suppression period followed for more 36 h, and then hatching occurred irregularly. When eggs were transferred to 25ºC constant, the hatching rhythm disappeared immediately (Fig. 8D, E). Hatching suppression lasted for more 70 h, and most eggs died with a few hatched.

When eggs were transferred from DD to LL (L-on single signal) on day 9 days at 25ºC constant, although a few nymphs hatched out after L-on (Fig. 9A-a), a hatching peak was obscure (Fig. 9A-b). When they were given L-on single signal on day 17 at 15ºC, hatching occurred within 2 h after L-on (Fig. 9B). When eggs were exposed to a temperature increase from 15ºC to 25ºC (T-rise single signal), hatching occurred within 2 h after T-rise under DD (Fig. 10A) and LL (Fig. 10B).

Eggs were transferred from LL to DD (L-off single signal) at 25ºC, hatching did not occur after L-off and eggs hardly hatched thereafter (Fig. 11A). At 15ºC, only a few nymphs hatched out or not after L-off and a clear peak was not always observed (Fig. 11B). When eggs were transferred from 25ºC to 15ºC, the mean time of hatching (± SE) occurred 8.4 h ± 0.8 h (Fig 12A) or 7.1 h ± 0.7 h (Fig. 12B) after T-fall under DD or LL, respectively.

## DISCUSSION

The hatchability was very low under DD and LL at 25C and 20C, where embryos of *C. bonneti* developed to a stage of hatching. However, it increased under photoperiods. Similar results were obtained with *E. engelhardti subtropica* (Arai 1977a). In contrast, the hatchability of *G. buergeri* (Arai 1979c) and *H. jezoensis* (Arai 1998b) were high by any photoperiods at 25ºC and 30ºC. Therefore, even though these species inhabit the same environment, favorable hatching temperatures apparently differ between species. The hatchability also increased under thermoperiod (25ºC: 15ºC).

Egg hatching, adult emergence, and behavior in many insect species, are synchronized with environmental cycles (Saunders 2002). In C. bonneti, hatching was sporadic under DD and LL at constant temperatures, but it was synchronized under photoperiodic conditions. If hatching simply occurs in response to L-on, it should occur only after L-on. However, a few nymphs hatched before L-on under LD 12: 12 at 25ºC and 20ºC.

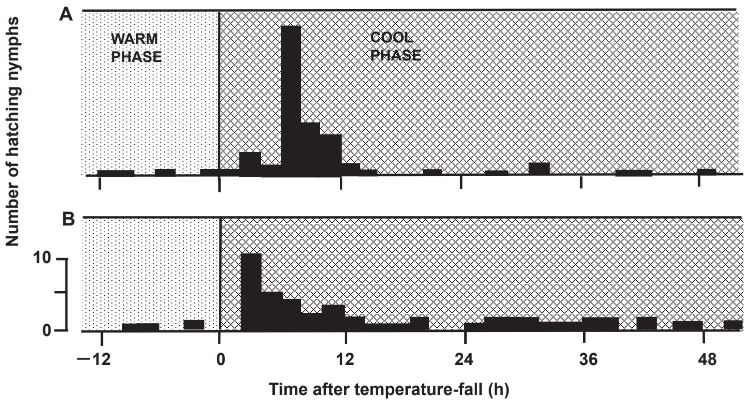

Figure 12 Effects of a single signal of T-fall (from 25ºC to 15ºC) under DD (A) and LL (B) on the timing of egg hatching of *Chizuella bonneti*. Each treatment comprised 300 eggs.

Therefore, it was thought that the hatching time of C. *bonneti* had already been determined by the previously given photoperiodic signals. The involvement of L-on and L-off signals in determining the hatching time has been reported for *E. engelhardti subtropica* (Arai 1977a, 1979a), *G. buergeri* (Arai 1979c), and *H. jezoensis* (Arai 1998b). The involvement of the L-off single signal has also been reported for *E. engelhardti subtropica* (Arai 1977a, 1979a) and *G. buergeri* (Arai 1979c). In *C. bonneti,* however, the involvement of L-off single signal in determining the hatching time was not clear.

The hatching time of *C. bonneti* was also determined by thermoperiod. Under DD, hatching peak occurred around 12 h after-T-fall and many nymphs hatched within 2 h after T-rise under WC 6: 18, and before and after T-rise under WC 12: 12. Therefore, it was thought that the hatching time had already been determined by the previously given thermoperiodic signals. Under LL, when T-fall was set to 0:00, the mean hatching time and standard deviation (SD) in WC 6: 18 was 7.4 h ± 1.9 h and in WC 12: 12 was 5.3 h ± 2.6 h. Under WC 18: 6, hatching peaked before and after T-rise, and the mean hatching time and SD was 5.4 h ± 2.1 h. The time from T-fall to the peak of hatching tended to be longer as the cool phase was longer. These results suggested that both signals of T-rise and T-fall were involved in determining hatching time and the time-measuring system started by these signals was affected by the presence or absence of light.

The eggs of *C. bonneti* were hatched every day within 2 h after L-on under LD 12: 12 at 15ºC. When eggs were transferred from LD 12: 12 to DD or LL, hatching was inhibited for about 56 h after hatching in L-on, and hatching occurred sporadically thereafter. When eggs were exposed to WC 12: 12, hatched every day before and after T-rise or 4–6 h after T-fall under DD or LL, respectively. When eggs were transferred from WC 12: 12 to a constant temperature of 15ºC, the hatching peak occurred 10–12 h under DD or around 6 h under LL after the transition to constant temperature of 15ºC, and hatching was not observed for about 30 h, thereafter hatching was irregular. When eggs were transferred to a constant temperature of 25ºC, the daily rhythm of hatching disappeared immediately and most eggs died. Although the continuation of the hatching rhythm was not clear, the existence of the hatching suppression time suggests the involvement of endogenous rhythm and a time-measuring mechanism that is triggered by the photoperiodic or thermoperiodic signals in determining the timing of egg hatching. Similar results were also obtained for *E. engelhardti subtropica* (Arai 1977a) and *G. buergeri* (Arai 1979c). In *H. jezoensis,* a circadian rhythm was also observed under photoperiodic or thermoperiodic conditions (Arai 1998b). It suggested that endogenous rhythm is involved in determining the egg hatching time of katydid. It is thought that the persistence of endogenous rhythm varies from species, such as whether the hatching rhythm lasts for long time, disappears after several times, quickly loses its persistence, or does not persist at all.

In *C. bonneti,* egg hatching was triggered by a single signal of L-on or T-rise, similar to the trends observed in *E. engelhardti subtropica* (Arai 1977a, 1979a). However, the responses of *C. bonneti* to these single signals were weaker than those of *E. engelhardti subtropica.* In *G. buergeri,* hatching was not directly triggered by single signals of L-on or T-rise, but since hatching occurred synchronously with the photoperiodic or thermoperiodic conditions, hatching time is considered to have already been determined by these signals (Arai 1979c). Trigger of hatching behavior by L-on or T-rise varied among katydids. A similar phenomenon has been reported in the larval jumping behavior of mature larvae in the oriental fruit fly, *Bactrocera dorsalis* (*Dacus dorsalis*) (Arai 1975, 1976), whereby, the jumping behavior was triggered by L-on, such as lightning, T-fall due to rainfall, and vibrations due to falling fruit. Behaviors that are triggered by sudden disturbances stimulations have ecological importance and are thought to be related to mechanisms involved in avoiding disadvantages associated with sudden changes in the environment prior to hatching.

In the natural environment, some katydids of *C. bonneti, E. engelhardti subtropica* (Arai 1977a), *G. buergeri* (Arai 1979c), and *H. jezoensis* (Arai 1998b) hatch during the period of high humidity from night to dawn. This indicates that the hatched nymphs may emerge at the most convenient time to protect themselves from drying. Some species hatch without synchronizing with environmental cycles, such as the nymphs of *B. dorsalis* (Arai 1975, 1976) and the cucumber looper, *Anadevidia peponis* (Sasaki 1975), which hatch in fruits, and the nymphs of *N. triguttata* (Arai *et al.* 1994), which hatch in water, and thus emerge in environments with 100% humidity. Therefore, the timing of hatching of these species is considered to not be affected by the relative humidity in the air.

The various behaviors are synchronized with environmental cycles and most organisms that have evolved under a periodically changing environment have acquired the function of a biological clock (Bünning, 1960, 1973; Aschoff, 1965, 1981; Menaker, 1971; Saunders, 1978; Chiba & Takahashi, 1991). However, some behaviors are not synchronized with environmental cycles and the biological clock is not involved in determining the time of behaviors. It is considered that the choice of whether the behaviors are synchronized with the environmental cycles have been selected to occur at the most appropriate time for the species under the influence of pressure from various environmental factors, i.e. temperature, day length, humidity, population density, natural enemy, and so on. It was thought that the hatching of *C. bonneti* occurred at the most appropriate time of day by integrating incorporation of time-measuring mechanisms synchronized with environmental cycles, trigger of hatching behavior by signals of environmental changes, increase in hatchability due to environmental cycles, and so on.

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