

論文：

Determining factors of egg diapause of bivoltine in *Dianemobius csikii* Bolivar (Orthoptera: Trigonidiidae)

Tetsuo ARAI¹Yasuhiro MATSUNAGA²

Abstract

The beach ground cricket, *Dianemobius csikii* (Orthoptera: Trigonidiidae), collected from the mouth of the Kiyotake River, Miyazaki City, Miyazaki Prefecture, Japan (31.8°N, 131.5°E, 4.6 m elevation), is a bivoltine species and overwinters as the egg stage. This species has two wing forms, macropterous and brachypterous, and the macropterous rate at 28°C was higher in the long photoperiods. The effects of photoperiods on nymphal duration were small. The egg duration was affected by the rearing photoperiods of nymphs and adults and the egg-storing temperatures. The eggs were considered diapause eggs because when eggs were kept at 15°C for 20 weeks after oviposition, they were viable but did not hatch, regardless of the rearing photoperiods of nymphs and adults. At egg-storing temperatures of 20, 25, and 30°C, the egg duration showed two peaks, short and long, which were regarded as non-diapause and diapause eggs, respectively. The proportion of diapause eggs increased when the rearing photoperiods of nymphs and adults were short and egg-storing temperatures were low. When the rearing photoperiod of nymphs and adults was short, the diapause rate increased with increasing days after adult emergence. The egg diapause in *D. csikii* was determined by the rearing photoperiods experienced by nymphs and adults, egg-storing temperatures, and adult's days after emergence.

“Key words: adult's days after emergence, egg diapause, egg-storing temperature, nymphal duration, nymph and adult rearing photoperiods, wing form”

INTRODUCTION

Dianemobius csikii is distributed in Honshu, Shikoku, Kyushu, Tanegashima, Amami Oshima, and Tokunoshima in the Japanese archipelago, and also South Korea and north China (Ichikawa *et al.* 2006). This species is mainly found on highly pristine ocean beaches where *Vitex rotundifolia*, *Glehnia littoralis*, *Calystegia soldanella*, *Ischaemum antheperoides*, and other plants grow. It also inhabits the riverbeds of the Tenryū River and its tributaries, the Tōyama River (Yomo 2000, 2011) in the Nagano Prefecture, and the Jyoganji River in the Toyama Prefecture (Negoro 2012). In mainland China, *D. csikii* has been found in the fields of Datong City (approximately 40.1°N, 131.1°E) (Arai, unpublished), and is distributed in Beijing, Hebei, Inner Mongolia, Sichuan, Hainan, and Yunnan, and also in Taiwan (Liu *et al.* 2016).

Studies on *D. csikii* have mainly provided brief reports focusing on the relationship between body color and beach sand color, photoperiodicity of nymphal development (Masaki & Walker 1987; Walker & Masaki 1989), and investigations of substrate selection, mating behavior, and crypsis (Kuriwada 2022; Sato & Kuriwada 2022). However, little is known about its ecology and microhabitat selection. The small- or large-

scale alteration or disturbance of pristine sandy beaches inhabited by *D. csikii* is sometimes caused by natural disasters such as heavy rains, tsunamis, typhoons, and storm surges. However, the destruction of suitable habitats by sand compaction from car encroachment on beaches, beach pollution from campfires, beach litter dumping, and waste oil from ships and boats pose greater threats to *D. csikii* than natural disasters, and have a significant impact on its survival. Therefore, elucidation of the life history of *D. csikii* is very important to conserve its habitats.

The purpose of this study was to elucidate the ecology of *D. csikii* by investigating the effects of photoperiods on its wing form and nymphal development, and the impact of photoperiodical conditions under which the nymphs and adults are reared and egg-storing temperatures on the incidence of diapause. This would help the continued survival of the species and its conservation by identifying ecosystems, habitats, and areas that support its occurrence.

MATERIALS AND METHODS

Insects

Adults and nymphs of *D. csikii* were collected on sandy beaches at the mouth of the Kiyotake River, Miyazaki

(1) Niina 5-20-31, Mino City, Osaka, Japan 562-0005

(2) Nagayoshi-Rokutan 3-5-30, Hiranoku, Osaka, Japan 547-0016

City, Miyazaki Prefecture, Japan (31.8°N, 131.5°E, 4.0 m elevation), in June and September 2001, 2006, 2007, 2010, 2019, 2021, and 2022. The crickets were reared in the laboratory at Ashiya University, Yamaguchi Prefectural University, and the first author's home. They were provided insect feed (Oriental Kôbo K.K., Osaka, Japan) and carrots. Water was placed in a plastic tube with a diameter of 3 cm and length of 6 cm and plugged with absorbent cotton. Eggs were laid into the absorbent cotton in the tube.

Determination of wing form type

Wing form classification was determined by the length of the hindwings; macropterous when the hindwings were longer than the forewings, and brachypterous when vice versa.

Wing form and nymphal duration

Dianemobius csikii nymphs were transferred to 2-L glass beakers within 24 h of hatching from their eggs. The base of each beaker was filled to a depth of 1 cm with sand sterilized by boiling, and 10 sheets of folded filter paper (11 cm in diameter) were stacked to prevent contact between individuals during nymphal molting. Temperature control was performed in a constant-temperature room at $28 \pm 1^\circ\text{C}$. Individuals were reared under varying photoperiods from 11 h of light and 13 h of darkness (LD 11:13) to 16 h of light and 8 h of darkness (16:8). These photoperiods were regulated using a timer within a 60 cm cubic wooden box, equipped with an LED bulb serving as the light source. The nymphs were provided with the same insect food mentioned above, and water was supplied by a water tube. The number of adults, their sex, and wing form were determined every 24 h.

Egg duration

Eggs were laid in the cotton wool plugs of water-filled plastic tube and placed in incubators (Nihon Ikakikai K.K., Osaka, Japan) at 15, 20, 25, and 30°C within 24 h after oviposition. The hatched nymphs were counted every 24 h.

Determination of egg diapause

Eggs hatched within 50 days at 20°C and 30 days at 25 and 30°C after oviposition were considered non-diapause, and after that were diapause.

Relationship between egg diapause and days after emergence

Nymphs and adults were reared under LD 12:12 and 15:9 at $28 \pm 1^\circ\text{C}$. Eggs were collected once a week for 6 weeks and kept at 20 or 25°C , and after that the numbers of hatching were observed every 24 h.

Statistical analysis

All statistical analyses were performed using EZR-Version 2.7-1 (Kanda 2013). When two factors were compared, the data were analyzed using t-tests and χ^2 -tests. Data comparing three or more factors were

analyzed using repeated measures Analysis of Variance (ANOVA) with Tukey's and Bonferroni tests.

RESULTS

Wing form

In females, the macropterous rate was 0% under LD 11:13 and progressively increased with longer photophases (Figure 1). Moreover, the incidence of macroptery was significantly higher under LD 14:10 to 16:8 than under LD 11:13 to 13:11 (Bonferroni test, $P < 0.05$). In males, the macropterous rates under LD 11:13 and 12:12 were 0% and only increased slightly under LD 13:11–16:8, and there were no significant differences between photoperiods. This shows that the macropterous rate of females was significantly higher than that of males during photoperiods longer than LD 14:10 (χ^2 -test, $P < 0.05$).

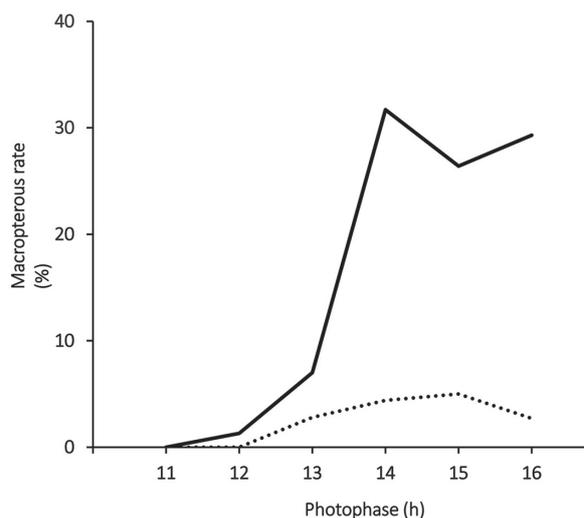


Figure 1. The macropterous rate of *Dianemobius csikii* under LD 11:13–16:8 at $28 \pm 1^\circ\text{C}$. Solid line: female. Dotted line: male.

Nymphal duration

The nymphal duration tended to be longer as the photoperiod became longer, however, no correlation was observed (Figure 2). The number of macropterous female individuals under LD 11:13–13:11 and in males under LD 11:13–16:8 was 0 or few, so nymphal duration could not be compared between wing forms (Table 1). Comparisons were only made when the sample size exceeded 10 individuals for the compared treatments. In comparisons between wing forms, the nymphal duration of macropterous females with LD 16:8 was slightly longer than that of brachypterous females (t-test, $P < 0.05$). However, there was no significant difference between wing forms for LD 14:10 and 15:9. Comparing brachypterous females and males, the nymphal duration of females under LD 14:10 was slightly longer than that of males (t-test, $P < 0.05$). However, there were no significant differences under the other photoperiods. In comparing the nymphal duration between photoperiods,

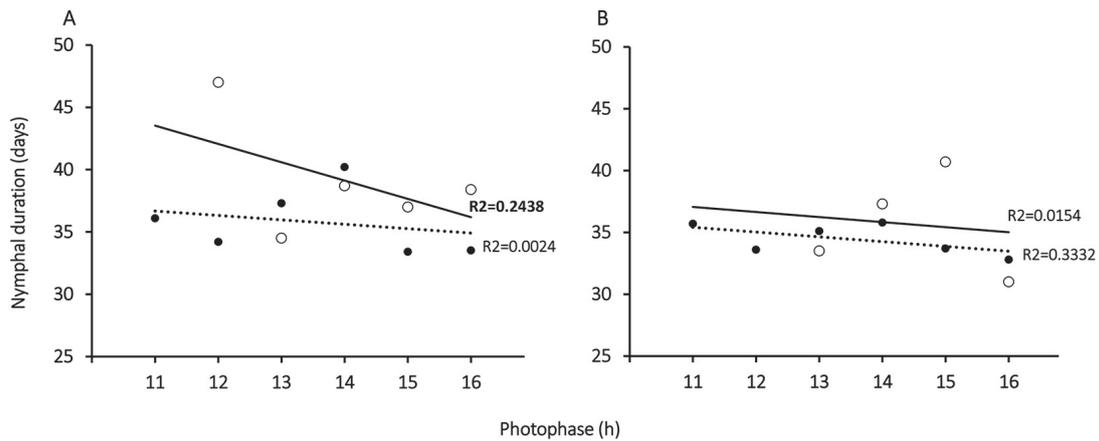


Figure 2. The nymphal duration of *Dianemobius csikii* under LD 11:13–16:8 at $28 \pm 1^\circ\text{C}$. A: female. B: male. White circle and solid line: macropterous form. Black circle and dotted line: brachypterous form.

Table 1 The nymphal duration of *Dianemobius csikii* under LD 11:13–16:8 at $28 \pm 1^\circ\text{C}$.

Sex	Photoperiod	Macropterous		Brachypterous		
		Light: Dark (h)	No of adults	Mean \pm SD	No of adults	Mean \pm SD
Female	11:13		0	–	77	36.1 \pm 5.8
	12:12		1	47.0	74	34.2 \pm 5.3
	13:11		4	34.5 \pm 1.9	53	37.3 \pm 8.0
	14:10		19	38.7 \pm 9.4	41	40.2 \pm 10.7
	15:9		19	37.0 \pm 8.9	53	33.4 \pm 7.3
	16:8		29	38.4 \pm 9.5	70	33.5 \pm 8.2
Male	11:13		0	–	63	35.9 \pm 4.3
	12:12		0	–	63	33.6 \pm 3.7
	13:11		2	33.5 \pm 0.7	69	35.1 \pm 6.2
	14:10		3	37.3 \pm 5.7	65	35.8 \pm 7.6
	15:9		3	40.7 \pm 13.9	57	33.7 \pm 4.0
	16:8		2	31.0 \pm 1.4	73	32.8 \pm 5.4

there was no significant difference in the female macropterous form under LD 14:10–16:8. In the brachypterous females, the nymphal duration under LD 14:10 was significantly longer than under LD 11:13, 12:12, 15:9, and 16:8 (Tukey's test, $P < 0.05$), although the other photoperiods were not significantly different. In the brachypterous males, the nymphal duration under LD 16:8 was significantly shorter than under LD 11:13 and 14:10 (Tukey's test, $P < 0.05$), although the other photoperiods were not significantly different.

Egg duration

Nymphs and adults were reared under LD 11:13 to 15:9, and the eggs these individuals produced were maintained at 15, 20, 25, and 30°C to determine the duration of egg development. Eggs kept at 15°C after oviposition did not hatch until 20 weeks, regardless of the rearing photoperiods of nymphs and adults. However, they were alive at that time and hatched when transferred to 25°C , suggesting that they were in diapause at 15°C . When eggs were kept at 20°C after oviposition and the

rearing photoperiods of nymphs and adults were LD 11:13–13:11, a small number of eggs hatched around 40 days later and the remaining eggs started hatching again at around 100 days. However, most of the eggs reared under LD 14:10 and 15:9 hatched at around 40 days (Figure 3A). When eggs were kept at 25°C, hatching was concentrated at around 18 days after oviposition when

the nymph and adult rearing photoperiods were LD 14:10 and 15:9, but when the photoperiods were shorter (LD 11:13–13:11), the number of hatching eggs decreased (Figure 3B). When eggs were kept at 30°C, over 60% of them hatched at around 13 days after oviposition, regardless of the photoperiod at which the nymphs and adults were reared (Figure 3C).

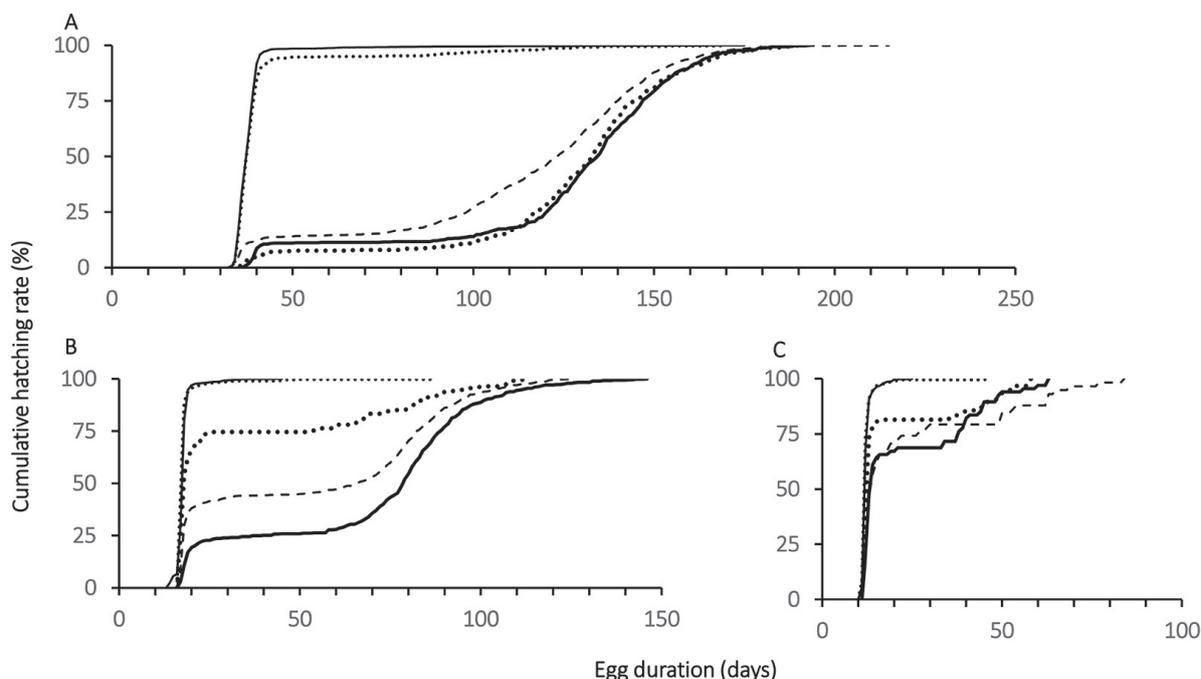


Figure 3. Effects of rearing photoperiods of nymphs and adults and egg-storing temperatures (A: 20° C; B: 25° C; C: 30° C) on the cumulative hatching rate of *Dianemobius csikii*. Nymphal and adult rearing photoperiods: Thick solid line: LD 11:13; Dashed line: LD 12:12; Thick dotted line: LD 13:11; Thin dotted line: LD 14:10; Thin solid line: LD 15:9.

The cumulative hatching curve showed that hatching was divided into two peaks. Therefore, the egg developmental duration was shown under various egg-storing temperatures and nymph and adult rearing photoperiods. Egg hatching at 20, 25, and 30°C was divided into two peaks, and there was a significant difference between the short and long egg developmental durations: eggs with a short and long developmental duration were considered non-diapause and diapause eggs, respectively (Figure 4). The egg durations of non-diapause and diapause eggs were shorter at higher temperatures (Tukey's test, $P < 0.05$) (Table 2). The developmental duration of non-diapause eggs under LD 11:13–13:11 at 20 and 25°C and LD 11:13 and 12:12 at 30°C was significantly longer than under LD 14:10 and 15:9 (Tukey's test, $P < 0.05$) (Figure 5). The number of diapause eggs tended to increase at lower temperatures and shorter photoperiods. The egg duration at 20 and 25°C was significantly longer at LD 11:13–13:11 than

at LD 14:10 and 15:9 (Tukey's test, $P < 0.05$), and at 30°C there were no significant differences between photoperiods. At each temperature, differences in the egg duration due to the rearing photoperiods of nymphs and adults were small, but they tended to decrease as the rearing photoperiods of nymphs and adults increased.

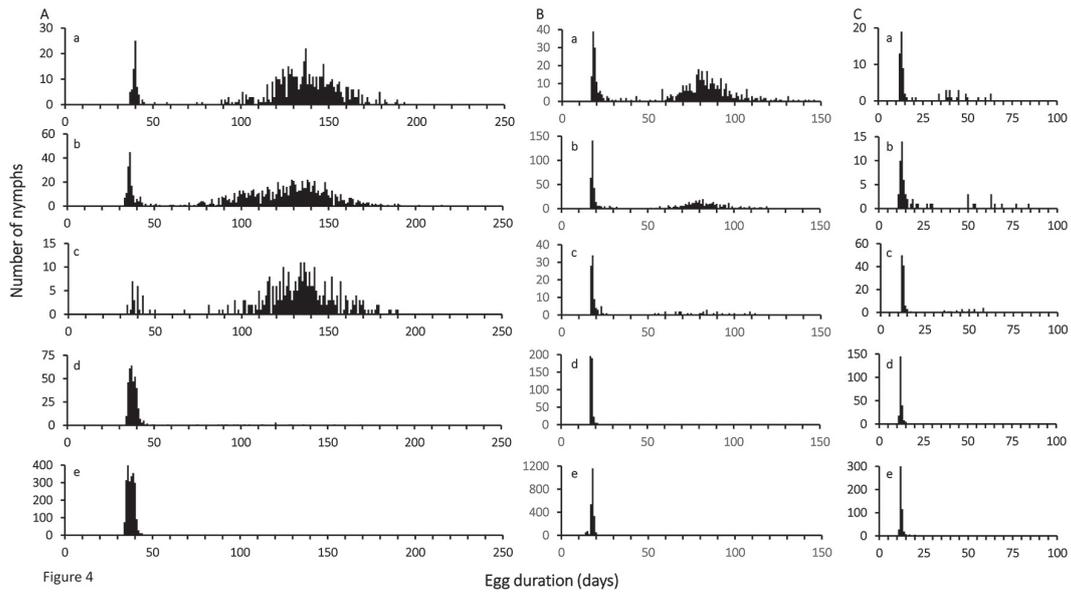


Figure 4. Effects of rearing photoperiods of nymphs and adults and egg-storing temperatures on the egg duration of *Dianemobius csikii*. A–C: egg-storing temperature at A: 20°C, B: 25°C, C: 30°C. a–e: rearing photoperiod of nymphs and adults under a: LD 11:13, b: LD 12:12, c: LD 13:11, d: LD 14:10, e: LD 15:9.

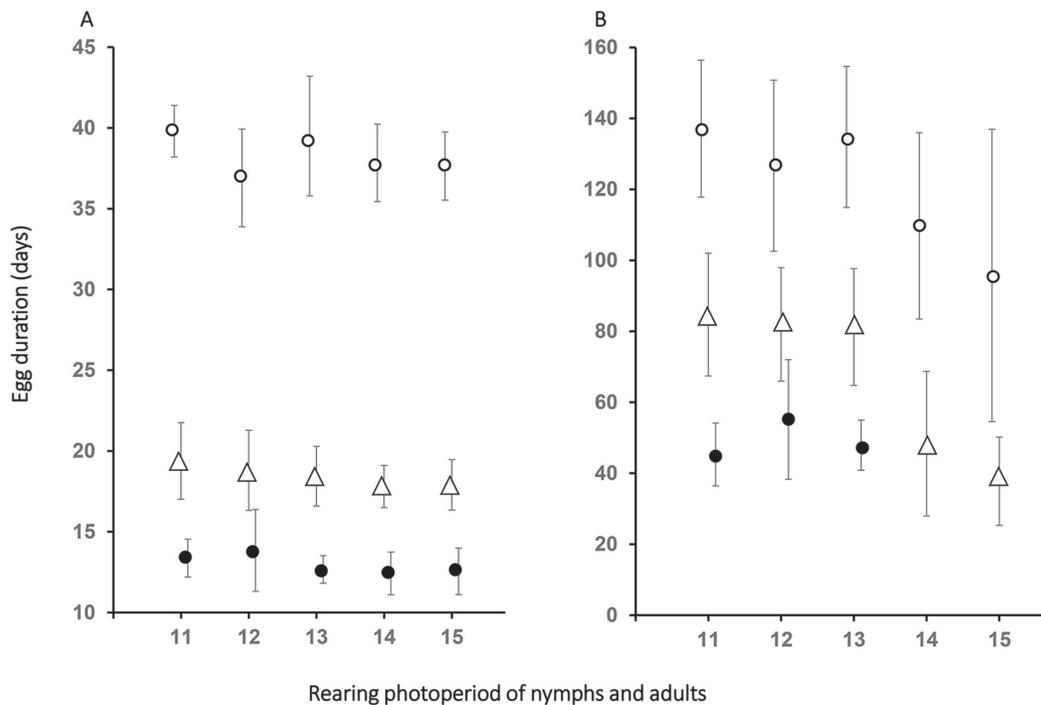


Figure 5. The egg duration of non-diapause and diapause of *Dianemobius csikii*. A: non-diapause egg. B: diapause egg. Black circle: egg-storing temperature 30°C. White triangle: 25°C. White circle: 20°C.

Table 2 The egg duration of *Dianemobius csikii* when nymphs and adults were reared under LD 11:13–15:9 at $28 \pm 1^\circ\text{C}$. The diapause eggs were defined as eggs that hatched by 50 days at 20°C and 30 days at 25 and 30°C , and non-diapause eggs were defined as having taken longer to develop.

Temperature ($^\circ\text{C}$)	Photoperiod Light: Dark (h)	Non-diapause		Diapause	
		No of eggs	Mean \pm SD	No of eggs	Mean \pm SD
20	11:13	64	39.8 ± 1.6	516	137.1 ± 19.3
	12:12	151	36.9 ± 3.0	924	126.7 ± 24.1
	13:11	26	39.5 ± 3.7	314	134.8 ± 19.9
	14:10	358	37.8 ± 2.4	20	109.7 ± 26.3
	15:9	2240	37.6 ± 2.1	34	95.7 ± 41.2
25	11:13	117	19.4 ± 2.4	370	84.7 ± 17.3
	12:12	297	18.8 ± 2.5	391	82.0 ± 16.0
	13:11	85	18.4 ± 1.9	29	81.2 ± 16.4
	14:10	427	17.8 ± 1.3	6	48.3 ± 20.4
	15:9	2292	17.9 ± 1.6	17	37.8 ± 12.5
30	11:13	46	13.4 ± 1.2	21	45.3 ± 8.8
	12:12	43	13.8 ± 2.5	15	55.1 ± 16.9
	13:11	101	12.7 ± 0.9	23	47.9 ± 7.1
	14:10	222	12.4 ± 1.3	0	–
	15:9	498	12.5 ± 1.4	0	–

Egg diapause

Egg diapause was determined by the rearing photoperiods of nymphs and adults and the egg-storing temperatures. When nymphs and adults were reared at 28°C and LD 11:13–15:9 and eggs were kept at 15°C , eggs underwent diapause, regardless of the rearing photoperiods of nymphs and adults. When the egg-storing temperature was 20°C , the diapause rates were 5.3 and 1.5% for nymphs and adults under the LD 14:10 and 15:9 rearing photoperiods, respectively, and they were 89.0, 86.2, and 93.0% under LD 11:13–13:11, respectively (Figure 6). The critical day-length for egg diapause at 20°C was estimated to be 13.5 h. At 25°C , the diapause rates of eggs produced by nymphs and adults reared under photoperiods of LD 14:10 and 15:9 were 1.4 and 0.7%, respectively, and these corresponding rates were 76.0, 56.8, and 25.4% under LD 11:13–13:11, respectively. At 30°C , the diapause rates under nymph and adult rearing photoperiods of LD 14:10 and 15:9 were both 0%, and were 31.3, 25.9, and 18.5% under LD 11:13–13:11, respectively. The diapause rate was higher when the rearing photoperiods of nymphs and adults were shorter and increased when the egg-storing temperature was higher.

In comparing the diapause rates between photoperiods, there was no significant difference between LD 13:11–13:11 at 20°C , and between LD 14:10 and 15:9,

and LD 14:10 and 15:9 at 25°C . However, there were significant differences in other cases (Bonferroni test, $P < 0.05$). At 30°C , there were no significant differences. In comparing the diapause rates between temperatures, under LD 11:13 and 12:12, the higher the temperature at which eggs were kept, the higher the diapause rate (Bonferroni test, $P < 0.05$). For LD 13:11 and 14:10, the diapause rate at the egg-storing temperature of 20°C was significantly higher than at 25 and 30°C (Bonferroni test, $P < 0.05$), but there was no significant difference between 25 and 30°C . At LD 15:9, the diapause rate at the egg-storing temperature of 20°C was significantly higher than that at 25°C (Bonferroni test, $P < 0.05$).

Nymphs and adults reared under LD 12:12 and 15:9 at $28 \pm 1^\circ\text{C}$, and eggs collected once a week for 6 weeks. The relationship between the days after adult emergence and egg diapause rate was investigated. When nymphs and adults were reared under LD 12:12 and eggs were kept at 20 or 25°C , the diapause rate increased with adult's days after emergence (Figure 7A), but not under LD 15:9 (Figure 7B). There was a correlation between adult's days after emergence and diapause rate, however, the relationship differed depending on the nymphs and adults rearing conditions.

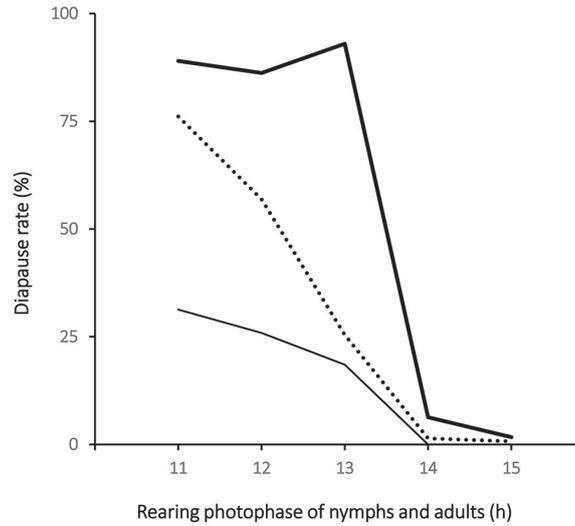


Figure 6. Diapause rates of *Dianemobius csikii*. Diapause eggs were defined as eggs that hatched by 50 days at 20°C and 30 days at 25 and 30°C, while the development of non-diapause eggs was longer. Egg-storing temperature: 20°C (thick solid line), 25°C (dotted line), 30°C (thin solid line).

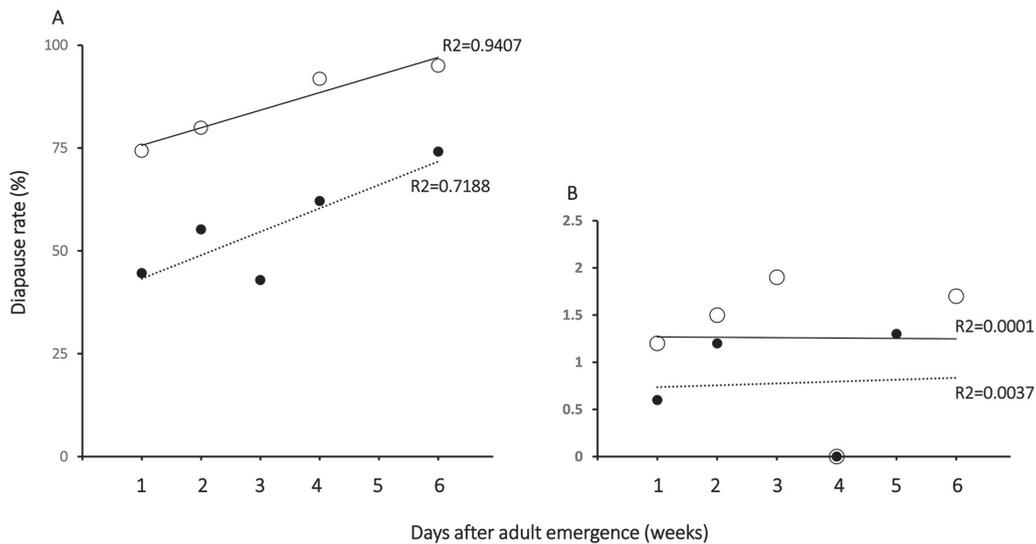


Figure 7. Relationship between egg diapause and days after adult emergence of *Dianemobius csikii*. A: Rearing under LD 12:12 at 28°C of nymphs and adults. B: LD 15:9. White circle: egg-storing temperature of 20°C. Black circle: 25°C.

DISCUSSION

Dianemobius csikii mainly inhabits sandy beaches on the seashore in the Japanese archipelago. The surface temperature of a sandy beach during the daytime in summer is considered 15–20°C higher than the ambient temperature, and these crickets may avoid these high temperatures by spending most of their time in the shade of plants and woody debris. The occurrence of nymphs and adults is affected by subtle environmental

factors such as sand conditions (size of sand grains and compactness of sandy beaches) and the presence or absence of vegetation and driftwood. They are thought to oviposit on sandy beaches, but there are still many unknowns about how their eggs withstand the hot and dry conditions of summer and the dryness of winter, and the mechanisms that determine egg diapause have not been extensively investigated.

At the mouth of the Kiyotake River, *D.csikii* overwinters as the egg stage and has a bivoltine life cycle. The

nymphal duration at 28°C was almost unaffected by the photoperiod. In our study, when nymphs and adults were reared under various photoperiods and the eggs were kept at 15°C after oviposition, all eggs the females produced underwent diapause, regardless of their developmental photoperiod. However, when eggs were kept at 20, 25, and 30°C, the hatching peaks were divided into short and long periods, representing non-diapause and diapause eggs, respectively. When nymphs and adults were reared under long day-length photoperiods, the number of non-diapause eggs increased, while the converse was true for diapause eggs, indicating that egg diapause was determined by the photoperiod under which nymphs and adults had been reared. Even under the same photoperiod, the proportion of non-diapause eggs or diapause eggs differed, depending on the egg-storing temperature, with the proportion of diapause eggs increasing with decreasing egg-storing temperature. These results indicate that egg diapause is determined by the photoperiod conditions under which nymphs and adults develop, and that the egg-storing temperature also plays a role in determining egg diapause. Insects with exogenous diapause, where diapause is triggered by environmental factors, adapt to new environments and expand their distribution by low-temperature resistance and changes in voltinism; this has been reported for *D. nigrofasciatus* (Masaki 1973) and *Polionemobius mikado* (Masaki 1978, 1979a, b). Endogenous diapause species are thought to expand their distribution by controlling their development with day length, and there is a series of detailed studies on geographical variation in the egg duration, nymphal duration, and body size in *Telleogryllus emma* (Masaki 1965, 1967).

The eggs of *D. csikii* in the Kiyotake River hatch after approximately 37 days at 20°C, 18 days at 25°C, and 13 days at 30°C awakening from diapause (Arai, unpublished). Overwintered eggs are considered to have hatched in mid-April, and since the nymphal duration is hardly affected by the photoperiod, the egg hatching is considered to be in mid-June. The nymphs develop under a long day length of 14 to 15 h, and the eggs that these adult females lay are exposed to high temperatures and become non-diapause. It was suggested that the hatching of the second generation began in early July and that adult emergence began in early September. The nymphs of the second generation are exposed to day lengths that shorten from 14 to 13 h, which are encountered when the mean and minimum temperature drops from 25°C and 22°C to 20°C and 18°C, respectively. Therefore, diapause egg production increases and most eggs become diapause, but some eggs may hatch. However, it is assumed that these nymphs do not emerge because winter temperatures are too cold for them to develop.

A decrease in voltinism is inevitable as a species moves to and settles in areas with shorter developmental periods during a range expansion. The egg diapause of *D. nigrofasciatus* was determined by the photoperiod of the nymphal stage and was bifurcated into two zones around 38°N in the Japanese archipelago, where photoperiodic responses of nymphal development differed between the

univoltine and bivoltine zones (Masaki 1973). The egg diapause of *D. csikii* was determined by the photoperiod during the nymphal stage in the same way as in *D. nigrofasciatus*. However, nymphal development was hardly affected by the photoperiod in both the univoltine and bivoltine zones, and in this respect, it differed from that in *D. nigrofasciatus*. Whether and how photoperiodic effects on nymphal development affect their range expansion and adaptation to new environments is unknown, but this raises very interesting issues that need to be clarified to better understand this process.

Egg diapause in *D. csikii* was determined using a two-step process. Firstly, egg diapause was determined by considering the photoperiod during an individual's nymphal development. In addition, the influence of adult's days after emergence on egg diapause suggests that it increases the survival rate of the population in Miyazaki. Secondly, the role of egg-storing temperature in determining egg diapause was considered. The fact that the photoperiod of the nymphal stage had little effect on nymphal development indicates that nymphal development is constant in this species, regardless of the season and latitude, ensuring the best use of the developmental period as possible. However, the relationship between photoperiodicity and changes in voltinism on nymphal development, and their effect on distribution expansion need to be clarified in the future.

Although the survival of *D. csikii* on highly natural sandy beaches is sometimes threatened by natural disasters, it seems more often than not that they are deprived of their habitat by anthropogenic effects. The limited knowledge of the biology of *D. csikii* addressed in this paper may contribute to the conservation of this species, which is listed as near-threatened or data deficient due to limited information in the Japanese prefectural Red Data Books. We hope this study will help clarify some aspects of the ecology of *D. csikii* and provide basic data for conserving this species and its habitat.

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