Seasonal Changes in the Incidence of Embryonic Diapause in the Band-Legged Ground Cricket, Dianemobius nigrofasciatus

Authors: Shiga, Sakiko, and Numata, Hideharu

Source: Zoological Science, 14(6) : 1015-1018

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.14.1015

ZOOLOGICAL SCIENCE 14: 1015–1018 (1997)

Seasonal Changes in the Incidence of Embryonic Diapause in the Band-Legged Ground Cricket, *Dianemobius nigrofasciatus*

Sakiko Shiga* and Hideharu Numata

Department of Biology, Faculty of Science, Osaka City University, Sumiyoshi, Osaka 558, Japan

ABSTRACT—The incidence of embryonic diapause in the band-legged ground cricket, *Dianemobius nigrofasciatus* was examined in regard to egg production by individual females both in the laboratory and in the field in Osaka, Japan. (1) Females were classified into three types: diapause egg-producers (laid only diapause eggs), nondiapause egg-producers (laid only nondiapause eggs) and mixed egg-producers (laid both diapause and nondiapause eggs). (2) The longer the photophase, the smaller was the incidence of diapause egg-producers, and the larger was that of the nondiapause egg- and mixed egg-producers. The critical day-length was between 13 and 14 hr. (3) The longer the photophase, the smaller was the incidence of diapause eggs laid by mixed egg-producers. (4) In the field, both nondiapause egg-producers and mixed egg-producers were observed from June to August. In September and October, most of the females were diapause egg-producers. The present findings revealed that adults of the overwintered generation occur from June to August and those of the first generation occur in September and October. The former adult females become mixed egg-producers or nondiapause egg-producers under long-day photoperiods, and the latter females become diapause egg-producers under short-day photoperiods.

INTRODUCTION

Maternal photoperiod controls embryonic diapause in the southern populations of the band-legged ground cricket *Dianemobius nigrofasciatus* in Honshu, the main island of Japan: female adults show a long day-type photoperiodic response. Females in the northern populations, however, lay diapause eggs irrespective of photoperiod (Kidokoro and Masaki, 1978). It has been deduced from the photoperiodic responses for the induction of embryonic diapause and for nymphal development that *D. nigrofasciatus* makes univoltine life cycles in the northern regions and bivoltine life cycles in the southern regions of Honshu (Masaki, 1972; Kidokoro and Masaki, 1978). Although differences in the photoperiodic response among different latitudinal populations could explain the life cycles of *D. nigrofasciatus* in the laboratory, no one has examined the seasonal occurrence of their diapause in the field.

Maternal photoperiodic control of embryonic diapause has been shown in some other orthopteran species, for example, the ground crickets *Pteronemobius* (=*Dianemobius*) *taprobanensis* (Masaki, 1979) and *Allonemobius socius* (Tanaka, 1986), the Australian plague locust *Chortoicetes terminifera* (Wardhaugh, 1986), the migratory locust *Locusta migratoria* (Hakomori and Tanaka, 1992) and the Senegalese grasshopper *Oedaleus senegalensis* (Diop, 1995). In most cases, diapause incidence was obtained from eggs laid by females reared in populations. Consequently, it is not clear whether the females are equal in production of diapause eggs under a certain photoperiod; i.e., whether a given diapause incidence indicates that the females are composed of diapause egg-producers (laying only diapause eggs), nondiapause egg-producers (laying only nondiapause eggs) and mixed egg-producers (laying both), or all females lay diapause eggs in an even rate.

In the present study, we collected adults at certain intervals in the field and observed the diapause incidence of their eggs to determine the seasonal occurrence of embryonic diapause in regard to eggs produced by individual females of *D. nigrofasciatus* in Osaka, a southern region of Honshu, Japan.

MATERIALS AND METHODS

The experiments were performed in 1994 and 1996. Adults of *D. nigrofasciatus* were collected in grassy sites in Toyonaka City, Osaka, Japan (34°50′N, 135°28′E) from June to October. Insects were fed on an artificial diet (Oriental Yeast, Tokyo), pieces of carrot and water *ad libitum*. In the laboratory at 25 ± 1°C, nymphs and adults were kept under a stationary photoperiod of light/dark (LD) 12:12, 13:11, 14:10 or 16:8. For insect rearing and diapause determination, we followed the method of Shiga and Numata (1996). Nymphs were reared in a group. When adult females emerged, they were paired with similar-aged adult males in a glass tube. Eggs within 24 hr after oviposition were collected 5 times at 5-day intervals. The collected eggs were incubated at 25 ± 1°C under LD 16:8, and diapause eggs were

* Corresponding author: Tel. +81-6-605-2573; FAX. +81-6-605-2574.

identified 13 days after oviposition.

To examine seasonal succession in the incidence of diapause eggs, adults of *D. nigrofasciatus* were collected every 9 days from June 24 to October 10 in 1994 and on June 29, July 23 and October 4 in 1996. Adults were kept outdoors in Osaka (34°41′N, 135°31′E). Their eggs were collected every day from 6 to 9 or 10 days after the adults were set outdoors. The eggs were maintained thereafter in the following conditions. In 1994, all eggs were kept in the laboratory (25 ± 1°C, LD 16:8). In 1996 the eggs were divided into two groups: one was kept in the laboratory and the other was kept outdoors. The diapause eggs were determined 13 days after oviposition, except for the autumn eggs (from the collection on October 4, 1996) kept outdoors, whose diapause was examined 26 days after oviposition.

RESULTS AND DISCUSSION

Figure 1 shows the numbers of diapause and nondiapause eggs laid by individual female adults raised from the egg stage in the laboratory at 25°C. The females which survived for 25 days or more and laid 10 or more eggs were used. Five representatives are shown in each photoperiod. The diapause incidence of eggs seemed not to vary with the age of the females. The average numbers of eggs (and standard deviation) laid by a female per day were 4.2 ± 2.2, 5.4 ± 2.6, 7.9 ± 2.8 and 7.1 ± 3.0 under LD 12:12, 13:11, 14:10 and 16:8, respectively (ANOVA, $P<0.05$). The females laid less eggs under short-day photoperiods than under long-day photoperiods [the Tukey test (Zar, 1984, pp 186–190), $P<0.05$, LD 12:12 vs. 16:16, LD 12:12 vs. 14:10 and LD 13:11 vs. 14:10]. Fecundity might change at different photoperiods, as reported in some other nondiapause insects (Philogène and McNeil, 1984).

We classified females according to the incidence of the diapause eggs: diapause egg-producers (laid only diapause eggs), nondiapause egg-producers (laid only nondiapause eggs) and mixed egg-producers (laid both diapause and nondiapause eggs). The longer the photophase, the smaller was the incidence of diapause egg-producers, and the larger the incidence of nondiapause egg- and mixed egg-producers (Fig. 2). The critical day-length was between 13 and 14 hr, which agreed with Mukonoso [34°45′N (Masaki, 1972)] and Hachioji populations [35°39′N (Kidokoro and Masaki, 1978)]. The longer the photophase, the smaller was the incidence of diapause eggs laid by mixed egg-producers (Fig. 2).

In 1994, we examined seasonal succession in the incidence of diapause eggs (Fig. 3). In summer, from June 24 to August 8, mixed egg-producers and nondiapause egg-producers coexisted. The proportion of nondiapause egg-producers was 15–68%. Thereafter, it was difficult to find adults in the field, and the numbers of females which we collected were less than 10 on August 17and 26 and September 4. Diapause egg-producers were first found among the adults caught on August 17. In autumn, the females mostly consisted of diapause egg-producers. From September 13 to October 10, the proportion of diapause egg-producers was larger than 81%. The remainder was mixed egg-producers, which laid a small percentage of nondiapause eggs.

The incidence of diapause eggs is to some extent modified by environmental conditions to which the eggs have been subjected. In addition to the maternal photoperiod, the tem-

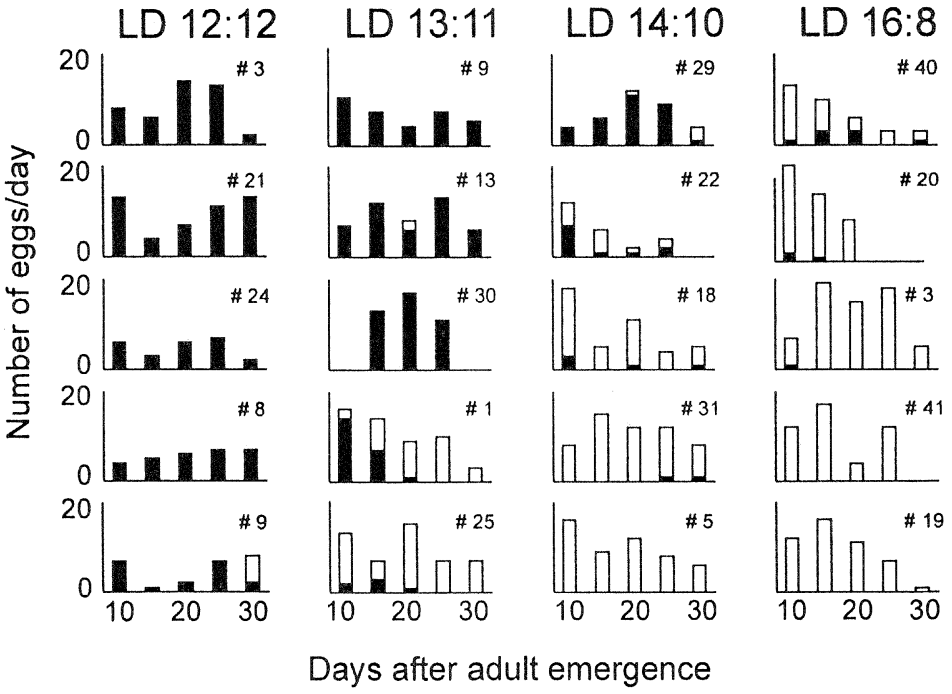

Fig. 1. Effects of maternal photoperiod on the induction of embryonic diapause in *Dianemobius nigrofasciatus*. Each graph shows the numbers of diapause (closed columns) and nondiapause (open columns) eggs laid by a female. Eggs laid for a day were collected 5 times at 5-day intervals from day 10 to 30. Five representatives for each photoperiod are shown.

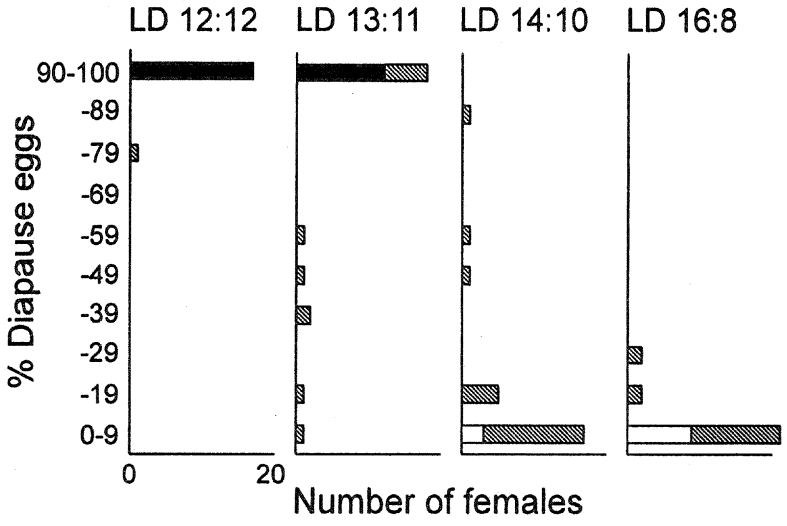

Fig. 2. Effects of maternal photoperiod on the induction of embryonic diapause in *D. nigrofasciatus*. Female adults were classified into 10 grades in terms of the incidence of diapause eggs (ordinate). The number of females in each grade is plotted (abscissa, maximum=20). Closed, hatched and open columns designate diapause egg-, mixed egg- and nondiapuse egg-producers, respectively. Results for all of the individuals that lived for 25 days or more and laid 10 or more eggs are shown. n=18-25.

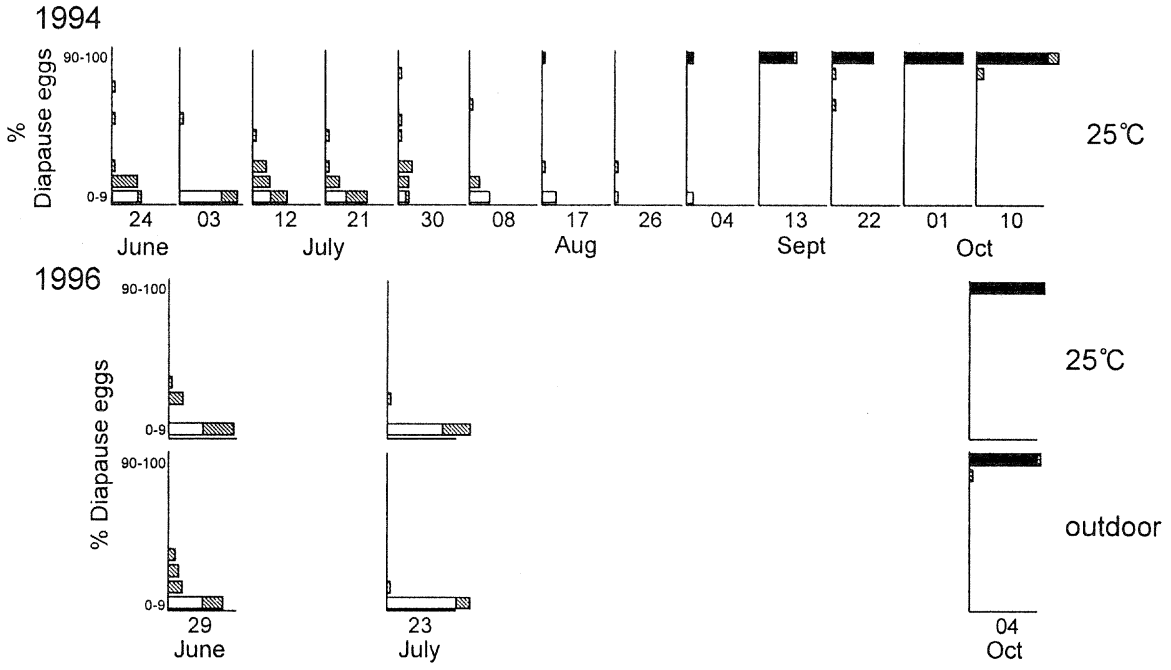

Fig. 3. Seasonal changes in the incidence of diapause eggs in *D. nigrofasciatus* in Osaka. About 20 pairs of adults were collected in the field every 9 days in 1994 and 3 times in 1996. All of the eggs from the adults collected in 1994 were kept in the laboratory (25°C, LD 16:8). The eggs from the adults collected in 1996 were divided into two groups: one group was kept in the laboratory (25°C, LD 16:8) and the other was kept outdoors. Females were classified into 10 grades in terms of the incidence of diapause eggs (ordinate). The number of females in each grade is plotted (abscissa, maximum=20). Closed, hatched and open columns designate diapause egg-, mixed egg- and nondiapuse egg-producers, respectively. Results for all of the individuals that laid 10 or more eggs are shown. Note that some females produced diapause eggs even in summer.

perature at which the eggs are maintained influences the incidence of embryonic diapause in some orthopterans (Masaki and Walker, 1987; Gregg, 1985; Tanaka, 1992). In 1996, therefore, the collected eggs were incubated in the laboratory (25°C, LD 16:8) or kept outdoors to examine the effect of egg-temperature on diapause. The average outdoor temperature ranged from 21.4 to 32.2°C, 28.8 to 33.8°C and 14.0 to 20.7°C during the egg incubation periods for the June 29, July 23 and

October 4 collections, respectively. Even under the outdoor temperatures, a small proportion of eggs entered diapause during summer (Fig. 3). The proportion of mixed egg-producers was larger in the June 29 than the July 23 collections in both the crickets kept in the laboratory and those kept outdoors. Almost all females collected on October 4 laid only diapause eggs. There was no significant difference in the incidence of diapause eggs between the laboratory and outdoor groups (the Mann-Whitney test, $P>0.1$).

Kidokoro and Masaki (1978) deduced the bivoltine life cycles of *D. nigrofasciatus* in the southern regions of Honshu from two separate photoperiodic responses for the induction of embryonic diapause and for nymphal development. The present study also revealed a bivoltine life cycle in the field in Osaka. A marked decrease in the number of adults was observed from late August to the middle of September. This presumably means that the adults present from June to August are the overwintered generation and those in September to October are the first generation of the current year. The natural daylength from late August to the middle of September in Osaka reaches 13 to 14 hr, which corresponds to the critical daylength at 25°C. Consequently, the overwintered generation receives long-day photoperiods and becomes mixed egg-producers or nondiapause egg-producers, and the first generation receives short-day photoperiods and becomes diapause egg-producers.

Seasonal changes of the egg production by individual females in bivoltine species were examined in *L. migratoria* (Tanaka, 1994) and *C. terminifera* (Wardhaugh, 1986); in both of these locusts, all of the females in summer were nondiapause egg-producers. In *D. nigrofasciatus*, however, mixed egg-producers occurred in summer. Although we did not follow the diapause eggs until their hatching, they looked healthy and were easily distinguished from non-viable eggs. The occurrence of mixed egg-producers in summer suggests that *D. nigrofasciatus* may partly have univoltine population in Osaka. The determination of whether the diapause eggs laid by a summer population overwinter and hatch in the next spring or hatch with a slight delay is the next step in the identification of the adaptive significance of the *D. nigrofasciatus* mixed egg-producers during summer.

REFERENCES

Diop T (1995) Effets de la photopériode sur l'induction de la diapause embryonnaire du criquet sénégalais, *Oedaleus senegalensis* (Krauss, 1877) (Orthoptera, Acridoidea). J Afr Zool 109: 161–172

Gregg P (1985) Reversal of embryonic diapause in the Australian plague locust, *Chortoicetes terminifera* (Walker), by temperatures above the development threshold. J Insect Physiol 31: 959–962

Hakomori T, Tanaka S (1992) Genetic control of diapause and other developmental traits in Japanese strains of the migratory locust, *Locusta migratoria* L.: Univoltine vs. bivoltine. Jpn J Entomol 60: 319–328

Kidokoro T, Masaki S (1978) Photoperiodic response in relation to variable voltinism in the ground cricket, *Pteronemobius fascipes* Walker (Orthoptera: Gryllidae). Jpn J Ecol 28: 291–298

Masaki S (1972) Climatic adaptation and photoperiodic response in the band-legged ground cricket. Evolution 26: 587–600

Masaki S (1979) Climatic adaptation and species status in the lawn ground cricket. I. Photoperiodic response. Kontyu 47: 48–65

Masaki S, Walker TJ (1987) Cricket life cycles. Evol Biol 21: 349–423

Philogène BJR, McNeil JN (1984) The influence of light on the non-diapause related aspects of development and reproduction in insects. Photochem Photobiol 40: 753–761

Shiga S, Numata H (1996) Effects of compound eye-removal on the photoperiodic response of the band-legged ground cricket, *Pteronemobius nigrofasciatus*. J Comp Physiol A 179: 625–633

Tanaka H (1994) Embryonic diapause and life cycle in the migratory locust, *Locusta migratoria* L. (Orthoptera: Acrididae), in Kyoto. Appl Entomol Zool 29: 179–191

Tanaka S (1986) Developmental characteristics of two closely related species of *Allonemobius* and their hybrids. Oecologia 69: 388–394

Tanaka S (1992) The significance of embryonic diapause in a Japanese strain of the migratory locust, *Locusta migratoria* (Orthoptera, Acrididae). Jpn J Entomol 60: 503–520

Wardhaugh KG (1986) Diapause strategies in the Australian plague Locust (*Chortoicetes terminifera* Walker). In "The Evolution of Insect Life Cycles" Ed by F Taylor, R Karban, Springer-Verlag, New York, pp 89–104

Zar JH (1984) Biostatistical Analysis. 2nd ed, Prentice Hall, Englewood Cliffs, NJ

(Received April 24, 1997 / Accepted August 6, 1997)