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Authors: Kobayashi, Shumpei, and Numata, Hideharu

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Effects of Temperature and Photoperiod on the Induction of Diapause and the Determination of Body Coloration in the Bean Bug, *Riptortus clavatus*

Shumpei Kobayashi and Hideharu Numata*

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

ABSTRACT—The incidence of diapause and details of body coloration were examined in adults of the bean bug, *Riptortus clavatus* (Thunberg) (Heteroptera, Alydidae) under various photoperiodic and temperature conditions. The insects showed a long-day photoperiodic response for the induction of diapause at 20, 25 and 30°C. However, some adults at 30°C failed to enter diapause even under short-day conditions. A photoperiodic response that produced light-colored adults under long-day conditions was common among 20, 25 and 30°C, although high temperature increased the proportion of light-colored adults. The photoperiodic response curve for the induction of diapause and that for in the determination of the coloration of the lateral metathorax exhibited a high degree of similarity at 20, 25 and 30°C, supporting a common time-measurement system for these two responses. With respect to the coloration of the ventral metathorax, temperature rather than photoperiod was the major determinant, although an effect of photoperiod was also detectable. There was no significant correlation between the lateral and ventral coloration in the threshold zone.

INTRODUCTION

In many insects, photoperiod controls both diapause and morphological polyphenism [21]. In most cases, the critical daylength is common to the two photoperiodic responses (e.g., [4, 7, 12, 22]). However, the critical daylength for diapause and that for morphological polyphenism are different in *Eysarcoris parvus* [23], *Sasakia charonda* [10] and *Aquarius paludum* [8]. Furthermore, in *Plautia stali* (Heteroptera, Pentatomidae), the induction of adult diapause is a photoperiodic response with a distinct threshold, while the determination of nymphal body coloration is a graded photoperiodic response with no distinct threshold of photophase [20]. Thus, the relation between the photoperiodic response for diapause and that for morphological polyphenism varies among insect species.

In an earlier study, we compared two photoperiodic responses, namely, the determination of seasonal forms and the induction of adult diapause in the bean bug, *Riptortus clavatus*, at 25°C [13]. We suggested the existence of a common time-measurement system for these two responses because the photoperiodic response curves for the two phenomena were similar [13]. Temperature has been shown to be a factor modifying photoperiodic responses in many insects [2, 21]. If we could show that the two responses in *R. clavatus* exhibit a similar dependence on temperature, we would be more confident in the validity of the above hypothesis. In the present study, therefore, we examine the effects of temperature on these two photoperiodic responses. Although the coloration of various body parts of adult bean bugs differs among photoperiodic conditions, we used the white spots on the lateral metathorax as the sole index of the seasonal form in the previous study because the effect of the photoperiod is most evident in this region [13]. In the present study, we also monitor the coloration of the ventral metathorax to take into account the possibility of regional differences in the determination of coloration.

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* To whom reprint requests should be addressed.

MATERIALS AND METHODS

Insects

Adults of *R. clavatus* were collected in legume fields in Kyoto City, Japan (35°00′N, 135°45′E) and their progeny was used for the experiments. Nymphs were reared, as described earlier [18], under 10L-14D, 12L-12D, 13L-11D, 13.5L-10.5D, 14L-10D or 16L-8D at 20 or 30±1°C. After emergence, isolated pairs of male and female adults were reared in 200-ml plastic cups.

Diapause status

Ten days (at 30°C) or 20 days (at 20°C) after emergence, the adults were dissected and their diapause status was assessed. If no yolk was deposited in the oocytes, the female was judged to be in diapause [18]. Similarly, if the width of the erection fluid reservoir, the sac of the ectodermal accessory gland, was less than 1 mm, the male was judged to be in diapause [19].

Body coloration

Body coloration was examined after the assessment of the diapause status. We classified the coloration of the lateral metathorax by the method of Kobayashi and Numata [13] (Fig. 1). We classified males into five grades and females, which were darker and less variable in the coloration of the lateral metathorax than males, into only three grades. Males of grades 1-3 and females of grades 1-2 are referred to as summer forms, and males of grades 4-5 and females of grade 3 are referred to as autumn forms with reference to the seasonal prevalence in the field [13]. We examined the coloration of another body part also, namely, the white patches on the ventral metathorax. The gradation of coloration of the ventral

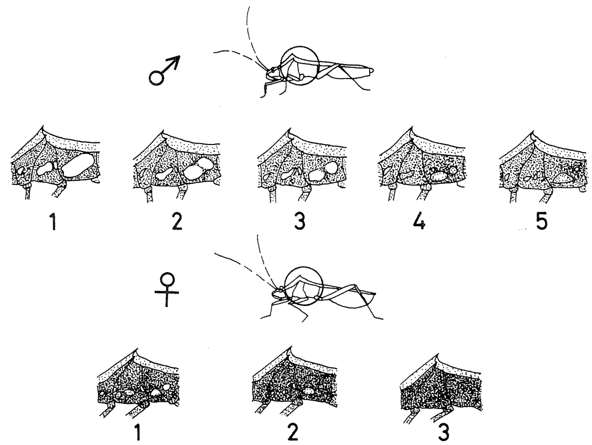

FIG. 1. Grades of coloration of the lateral metathorax in adult specimens of *Riptortus clavatus* [13]. Males: grade 1, a single large spot; grade 2, two spots separated by a thin line; grade 3, two spots that are clearly separated but without black dots in the center of the anterior spot; grade 4, two separate spots and some black dots in the center of the anterior spot; grade 5, the posterior spot is very small. Females: grade 1, two spots with no black dots; grade 2, two spots and some black dots in the anterior spot; grade 3, no posterior spot.

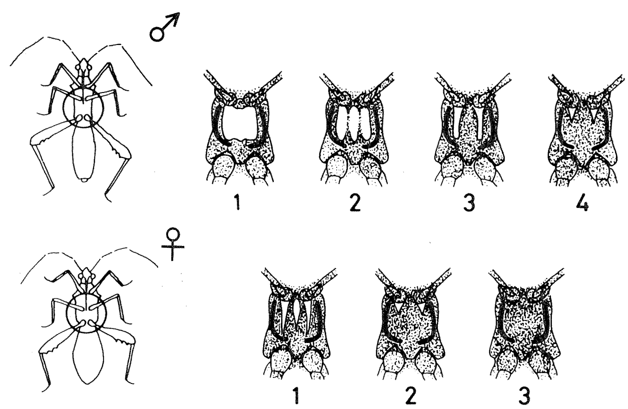

FIG. 2. Grades of coloration of the ventral metathorax in adult specimens of *Riptortus clavatus*. Male, grade 1, a single large white patch; grade 2, three separate white patches; grade 3, the central patch is absent and two white patches are present; grade 4, two small white patches. Female, grade 1, three separate white patches; grade 2, the central patch is absent and two small patches are present; grade 3, a very small white patch or none at all.

metathorax was continuous, resembling that of the lateral metathorax, and females were darker and less variable in the coloration of this portion also. Therefore we classified males into four grades and females into three grades (Fig. 2). In addition, we examined the coloration of the ventral metathorax in the individuals that had been reared at 25°C in the previous study [13], and we include results for the incidence of diapause and the coloration of lateral metathorax at 25°C from the previous study [13].

RESULTS

Induction of diapause

The insects showed a long-day photoperiodic response at each temperature. The photoperiodic response curves at 20°C and 25°C were similar (Fig. 3). At 30°C, however, some adults failed to enter diapause even under short-day conditions. In particular, the incidence of diapause was low under 12L-12D. However, remarkable stability with changes in temperature was observed in the critical day-length, which was about 13.5 hr in both sexes at each temperature examined.

Coloration of the lateral metathorax

The photoperiodic response that produces light-colored adults under long-day conditions was common at 20, 25 and 30°C in both sexes (Fig. 4). In males, however, some grade 4 adults emerged even under long-day conditions at 20°C, and some grade 1-3 adults emerged even under short-day conditions at 30°C. Under long-day conditions, the proportion of grade 3 adults was higher at 20°C than at 25°C or 30°C. Under short-day conditions, the proportion of grade 5 adults was lower at 30°C than at 20°C or 25°C. In females, some grade 1 and 2 adults emerged even under 12L-12D at 30°C. Thus, high temperature increased the proportion of light-colored adults while low temperature increased the proportion of dark-colored adults. However, the proportion of autumn forms was higher under 13L-11D than under 14L-10D in both sexes at each temperature as was observed in the incidence of diapause.

Coloration of the ventral metathorax

Temperature determined the coloration of the ventral metathorax rather than photoperiod (Fig. 5). At 30°C, most males were of grade 1–3 and most females were of grade 1 or 2 regardless of the photoperiod. At 25°C and 20°C, most males were of grade 3 or 4 and most females were of grade 2 or 3. Furthermore, the proportion of grade 4 males and grade 3 females was higher at 20°C than at 25°C. We will refer to grade 4 males and grade 3 females as low-temperature forms. Photoperiod also had some effect on the coloration of the ventral metathorax. In males at 20°C or 25°C and in females at 20°C, the proportion of low-temperature forms decreased as the photophase increased from 12 to 14 hr.

Relationship between lateral and ventral coloration

Under 13.5L-10.5D at 25°C, we found males with all grades of both lateral and ventral coloration. There was no significant correlation between the grade of lateral coloration and that of ventral coloration (Kendall's correlation coefficient by ranks, $\tau=0.03$, $P>0.75$) (Table 1).

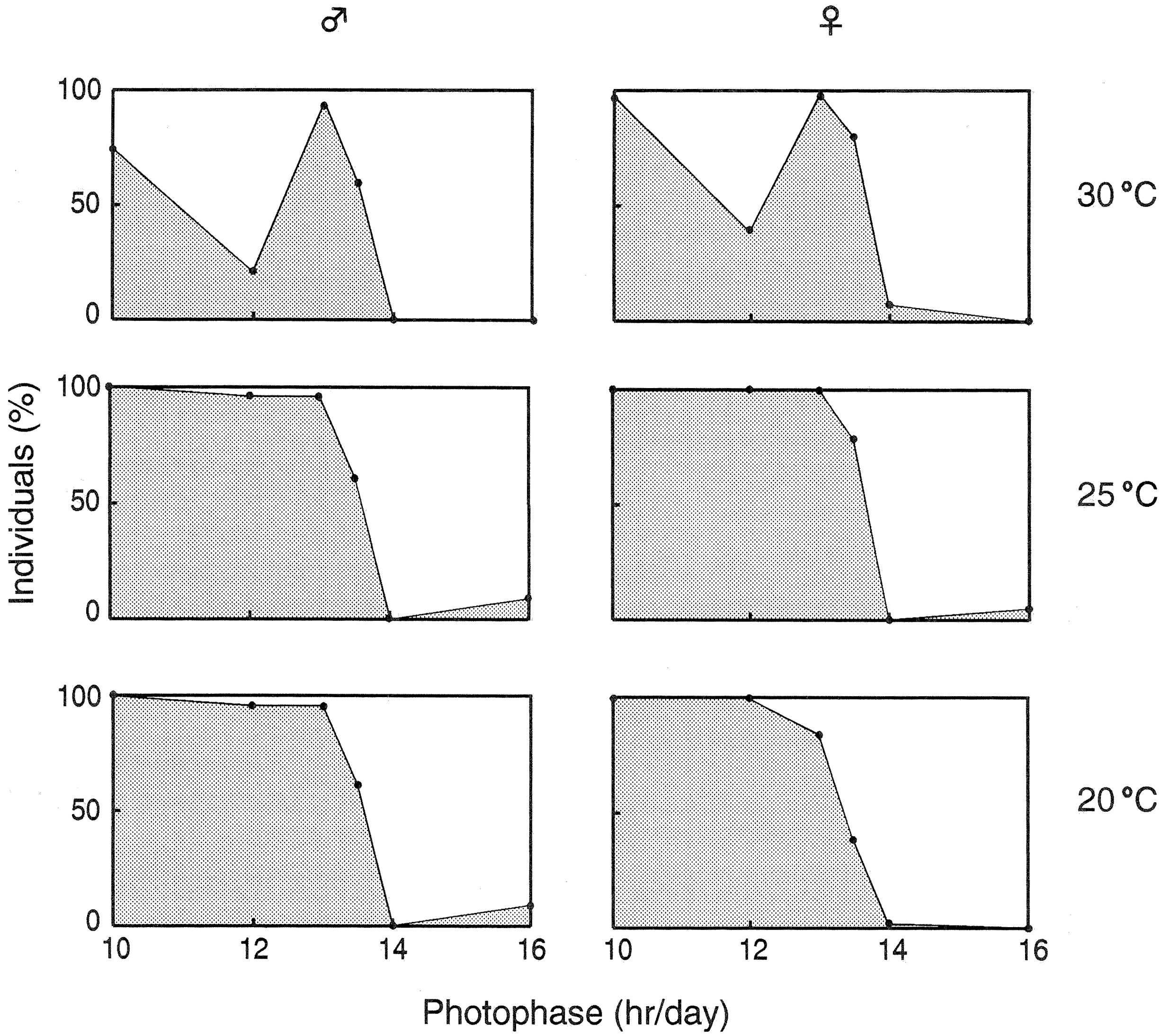

FIG. 3. Effects of temperature on the photoperiodic response for the induction of adult diapause in *Riptortus clavatus*. n=26–55. Shaded areas indicate the diapause individuals. The results at 25°C are from Kobayashi and Numata [13].

DISCUSSION

Effect of temperature on the photoperiodic induction of diapause

Temperature can affect the expression of the photoperiodic clock and the induction of diapause in many ways. Temperature often modifies the extent of a response or they change the critical daylength. In many species with long-day photoperiodic responses, high temperature and long-day conditions act together to avert diapause, whereas low temperature and short-day conditions act together to induce it [2, 21]. In *R. clavatus*, high temperature acts to avert diapause to some degree under short-day conditions although, in the present study, low temperature had little effect on the induction of diapause under long-day conditions (Fig. 3). Temperature changes the critical daylength in many species. In some insects, however, temperature has little effect on critical daylength and, therefore, these species exhibit a temperature-compensated response over practically the entire range of ecologically relevant temperatures [2, 21]. Between 20°C and 30°C, *R. clavatus* exhibited remarkable stability in the critical daylength for the induction of diapause (Fig. 3). This stability is useful for fixing the date at which natural populations enter diapause regardless of the ambient temperature during the autumn of any particular year.

Time-measurement system for the photoperiodic responses

We showed previously that in R. clavatus the photoperiodic response curve for the induction of diapause is similar to that for the determination of coloration of the lateral metathorax at 25°C, even though reproductive status and seasonal form are not perfectly correlated. Under photoperiodic conditions close to the critical daylength, there is a close relationship between diapause and the coloration of the lateral metathorax. From these results, we suggested a common time-measurement system for these two responses

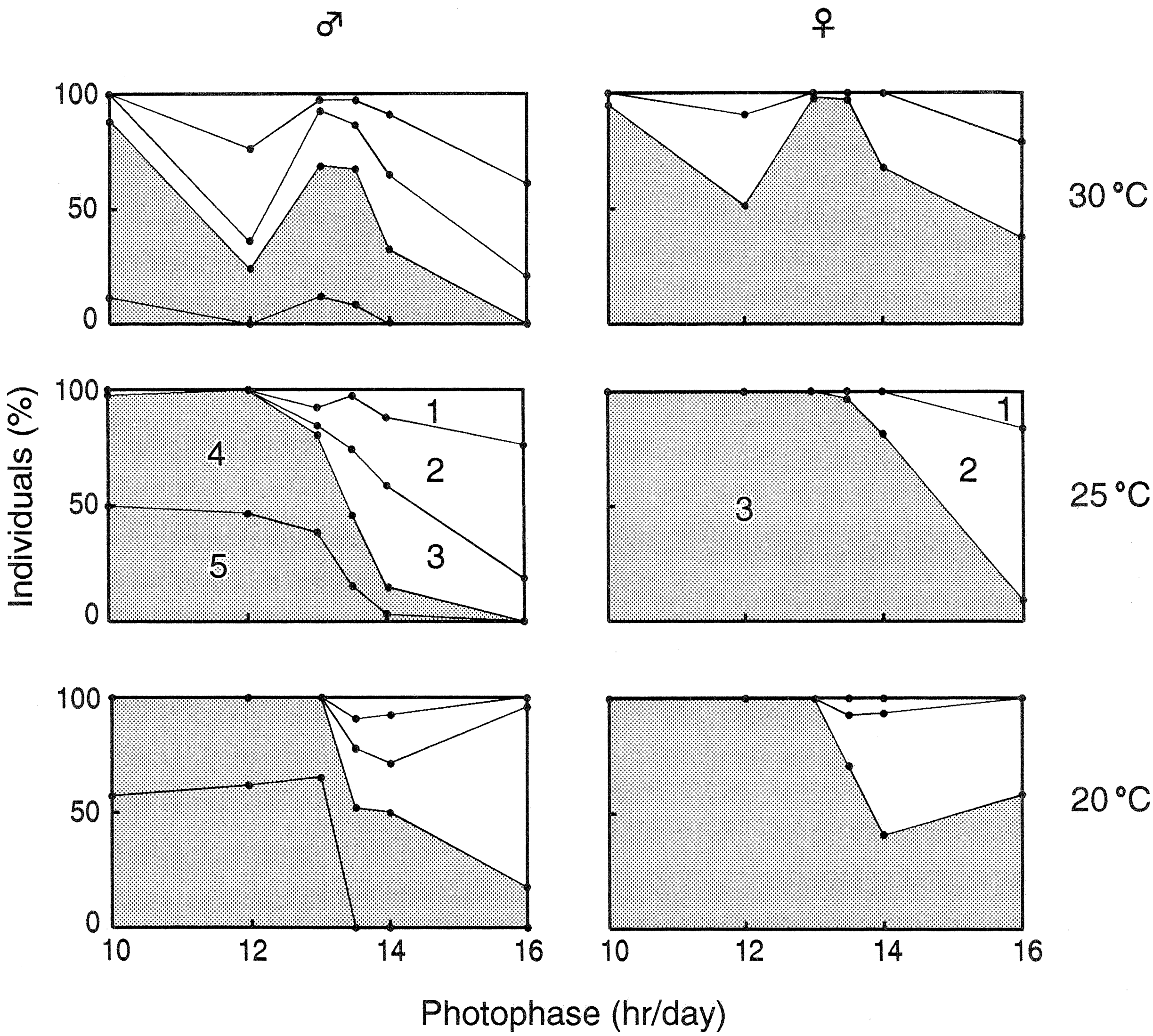

Fig. 4. Effects of temperature and photoperiod on the coloration of the lateral thorax in *Riptortus clavatus*. Numerals on the graph refer to grades of coloration (see Fig. 1). Shaded areas indicate the autumn forms. n=26–55. The results at 25°C are from Kobayashi and Numata [13].

[13]. The two photoperiodic response curves exhibiting a high degree of similarity at a higher or a lower temperature (Figs. 3 and 4) support our earlier hypothesis. With respect to the coloration of the ventral metathorax, temperature rather than photoperiod was the major determinant (Fig. 5). However, an effect of photoperiod was also detectable, and the proportion of low-temperature forms decreased as the photophase increased from 12 to 14 hr in males at 20°C or 25°C and in females at 20°C (Fig. 5). Consequently, it seems possible that a common time-measurement system might play a significant role in the determination of the coloration of the ventral metathorax also.

Effects of temperature and photoperiod on body coloration

Seasonal morphological forms have been described in many insects and, in most such cases, photoperiod is the decisive environmental factor involved [21]. For example, McPherson [17] revealed that the two adult forms of *Euschistus tristigmus tristigmus* (Heteroptera, Pentatomidae), which had previously been regarded as two different species, are examples of seasonal dimorphism that is actually controlled by photoperiod. In *R. clavatus*, photoperiod was the principal determinant of the coloration of the lateral metathorax, although temperature had some effect on the coloration (Fig. 4). Temperature also modifies the body coloration controlled primarily by photoperiod in some species of Lepidoptera, for example, *Polygonia c-aureum* [7, 9], *Lycaena phlaeas daimio* [5] and *Eurema hecabe* [11]. In *Podisus maculiventris* (Heteroptera, Pentatomidae), by contrast, temperature affects the seasonal variation in the black pigmentation in the abdominal terga, and photoperiod has a little or no effect on this characteristic [1]. Temperature rather than photoperiod predominantly determined the coloration of the ventral metathorax in *R. clavatus*, and low temperature

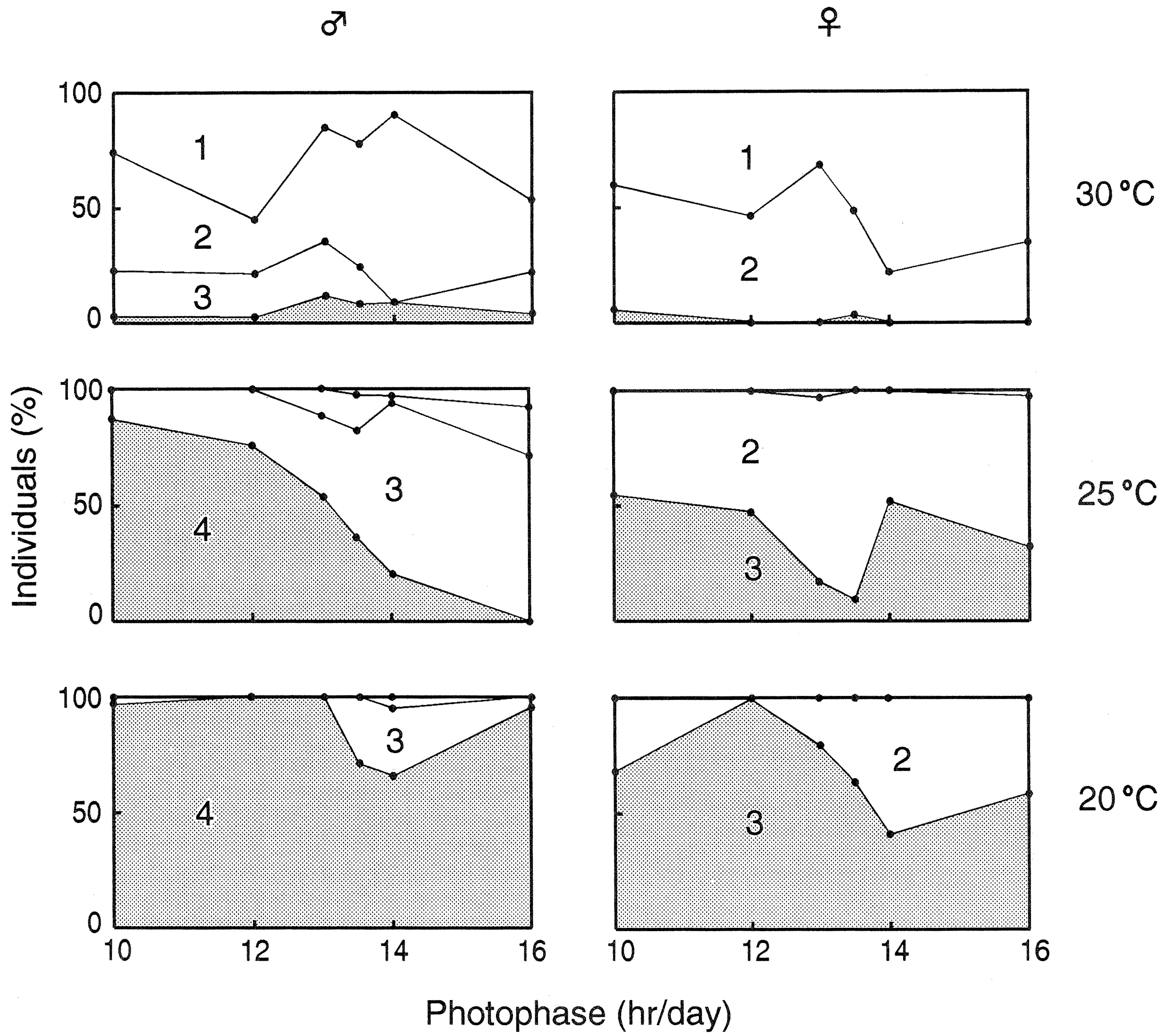

FIG. 5. Effects of temperature and photoperiod on the coloration of the ventral metathorax in *Riptortus clavatus*. Numerals on the graph refer to grades of coloration (see Fig. 2). Shaded areas indicate the low-temperature forms. n=26–55.

TABLE 1. Relationship between lateral and ventral coloration in male adults of *Riptortus clavatus* under 13.5L-10.5D at 25°C

Grade of ventral coloration	No. of individuals: Grade of lateral coloration 1	2	3	4	5	Total
1	0	0	0	1	0	1
2	0	0	4	2	0	6
3	1	5	3	6	2	17
4	0	4	4	3	4	15
Total	1	9	11	12	6	39

induced dark-colored adults, as is the case in *P. maculiventris* (Fig. 5).

Thus, in *R. clavatus*, temperature and photoperiod have different effects on the coloration of the lateral metathorax and that of the ventral metathorax. Furthermore, no significant correlation was observed between the lateral and the ventral coloration in the threshold zone (Table 1). The hormone(s) responsible for the determination of seasonal forms has been identified in some species of Lepidoptera (review, [14]). In *Araschnia levana*, the timing of ecdysteroid release controls the seasonal dimorphism of adult color pattern [15]. In contrast, in *P. c-aureum* it is summer-morph-producing hormone, a peptide secreted from the neurosecretory cells in the pars intercerebralis of the brain, that determines the dimorphic coloration [6]. If one hormone exclusively determines the body coloration in *R. clavatus*, there must be a similar tendency of response to photoperiod and temperature between the lateral and ventral coloration. In *L. phlaeas daimio*, both a hormone from the brain and ecdysteroids are involved in the determination of adult seasonal forms. Photoperiod during the larval stage regulates the secretion of the hormone from the brain, whereas temperature during the early pupal period affects the timing of ecdysteroid secretion [3]. If a similar control system exists also in *R. clavatus* and two hormones affects the coloration of the lateral or ventral metathorax separately, we can explain the regional difference in the response to photoperiod and temperature. However, it is unlikely that ecdysteroids are involved in the determination of adult body coloration in *R. clavatus*, because no difference can be found in the titer of hemolymph ecdysteroids during the fifth (final) nymphal instar between long-day and short-day conditions [16]. Further studies are needed to clarify the mechanism for the determination of body coloration in *R. clavatus*.

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