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Photoperiodic Control of Pre-Adult Development and Adult Diapause Induction in Zoophytophagous Bug *Dicyphus errans* (Wolff) (Heteroptera, Miridae)

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Abstract—Zoophytophagous plant bugs (Heteroptera, Miridae) increasingly attract interest as agents of biological plant protection. In the laboratory experiment, the effects of the day length and temperature on the duration of the pre-adult period and on induction of facultative winter adult diapause were studied in *Dicyphus errans* (Wolff, 1804) collected in Italy. The experiment demonstrated that at 20°C the duration of the pre-adult period of *D. errans* significantly depended on the day length. On average, females developed 1.3 days longer than males and, at the same time, the day length equally influenced the duration of the pre-adult period in both sexes. The pre-adult period was the shortest under short-day conditions (10 to 12 h of light per day), reached its maximum at day length of 14 h, but then decreased at 15 h, and at day length of 16 h it was as short as under short-day conditions. Also, a pronounced long-day type photoperiodic response of adult diapause induction was recorded in females of *D. errans* at 20°C: under short-day conditions (10 to 14 h of light per day) almost all females entered diapause, whereas under long-day conditions (15 and 16 h of light per day) about 90% of females were mature. The threshold of this photoperiodic response was close to 14 h 30 min. The mean (± S.D.) egg load of mature females was 6.3 ± 4.0 eggs per female and did not depend on the day length at which the female was reared before and after the final molt. When photoperiodic response of adult diapause induction was observed at two constant temperatures (20 and 25°C), the proportion of mature females depended significantly on the day length but not on the temperature: the shapes of the photoperiodic response curves of diapause induction were almost the same within the near-threshold zone at 20 and 25°C, i.e., the photoperiodic response was thermostable. The set of two photoperiodic responses manifested at different stages of the species' life cycle has an obvious adaptive significance. In Central Europe, *D. errans* has 2 or 3 generations per year and hibernates at the adult stage. Due to the thermostable photoperiodic response, females enter diapause always at the same time at the end of summer, regardless of the weather conditions of a particular year. When oviposition and pre-adult development are extended over a prolonged period in summer, nymphs from the later eggs might not be able to molt to adults in due time and then fully prepare for stable winter diapause. Under such circumstances, the photoperiodic response controlling the rates of pre-adult development acquires apparent adaptive meaning: with an autumnal shortening of the day length to 10–12 h, even under conditions of seasonal decrease in temperature, the rates of nymphal development increase and, thus, the chances of nymphs from the later eggs to molt to adults and properly prepare for overwintering also increase. The new data should be taken into account when analyzing the seasonal cycle of *D. errans* and developing the programs of mass rearing of this zoophytophagous mirid as an agent of biological plant protection.

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Many species of zoophytophagous plant bugs of the genus *Dicyphus* (Heteroptera, Miridae) currently attract interest as promising agents of biological plant protection in greenhouses. It was demonstrated that *Dicyphus tamaninii* Wagner, 1951 could control the western flower thrips *Frankliniella occidentalis* (Pergande, 1895) (Thysanoptera, Thripidae) on cucumber (Gabarra et al., 1995; Castañé et al., 1996), and that *Dicyphus hesperus* Knight, 1943 could control the greenhouse whitefly *Trialeurodes vaporariorum* West-

wood, 1856 (Homoptera, Aleyrodidae) on tomato (Sanchez et al., 2003). Combined application of *D. hesperus* and two parasitoid wasps, *Encarsia formosa* Gahan, 1924 (Hymenoptera, Aphelinidae) and *Eretmocerus eremicus* (Rose et Zolnerowich, 1997) (Hymenoptera, Aphelinidae), was shown to yield sufficient protection for tomato (Lambert et al., 2003). Techniques are being developed for using banker plants to facilitate the spreading of these bugs onto greenhouse vegetable crops (Lambert et al., 2003; Sanchez et al., 2003).

Dicyphus (*Dicyphus*) *errans* (Wolff, 1804) (Heteroptera, Miridae) is widely distributed in Europe (from the south of Scandinavia to the Mediterranean) and at the boundary of Europe and Asia (Kerzhner and Josifov, 1999; Wachmann et al., 2004). This bug is a polyphagous predator that feeds on small sucking plant pests, in particular aphids, whiteflies, thrips, their larvae and eggs, etc., and can obtain water from over 150 species of plants (Voigt, 2005; Ingegno et al., 2017). Due to its long legs and a number of morphological and behavioral adaptations, *D. errans* can live on pubescent plants that are avoided by many other predatory insects, which makes this bug a unique agent of biological plant protection (Southwood, 1986; Voigt, 2005; Voigt et al., 2007). Release of *D. errans* together with aphid parasitoids efficiently protected tomato in France, eliminating the need for pesticides (Lyon, 1986; Malausa and Trottin-Caudal, 1996). The species was also used for controlling tomato pests in Italy (Petacchi and Rossi, 1991, Quaglia et al., 1993; Wheeler, 2000; Ferracini et al., 2012).

To understand the biology and control mechanisms of the seasonal development of zoophytophages, and also to develop programs of laboratory rearing of plant protection agents, it is essential to know how environmental ecological factors, first of all the day length and temperature, affect the development of model species. Correspondingly, the goal of our work was to study the influence of the day length and temperature on the pre-adult development time and induction of facultative winter adult diapause in the zoophytophagous mirid bug *D. errans*.

MATERIALS AND METHODS

The laboratory strain of *D. errans* originated from two dozen bugs collected in 2013 in Tivoli (41°58′N, 12°48′E) and Ostia Antica (41°45′N, 12°18′E) on the outskirts of Rome (Italy). The experimental culture of *D. errans* was maintained at temperatures from 22 to 25°C and a photoperiod of 16L : 8D (16 h of light a day) on tobacco plants (*Nicotiana tabacum*, Virginia variety) in cages. The bugs were fed on eggs of the grain moth *Sitotroga cerealella* (Olivier, 1789) (Lepidoptera: Gelechiidae) and pollen, provided in excess.

Experiment No. 1: Assessment of the Effect of the Day Length on the Pre-Adult Development Time of Males and Females of Dicyphus errans at 20°C

The eggs and nymphs of *D. errans* used in this experiment were reared in covered 3.3-l plastic containers equipped with cloth (organza) access sleeves. At a temperature of 24°C and photoperiod of 16L : 8D, three tomato plants (Admiralteisky variety) with 7–9 leaves each were placed in each container and grain moth eggs were sprinkled in excess quantities onto the plants. Fertilized females of *D. errans* were released into the containers (on average 20 ind. into each) and left for 48 h to lay eggs into the tomato plant tissues. Then the females were removed and the containers with tomato plants and bug eggs were transferred into the experimental conditions (temperature 20°C and 7 different photoperiodic regimens: 10L : 14D, 11L : 13D, 12L : 12D, 13L : 11D, 14L : 10D, 15L : 9D, and 16L : 8D). The group of individuals reared in one container was treated as a cohort. Each of the 7 photoperiodic regimens was tested in 6 replications (i.e., 6 cohorts). The hatched nymphs were fed three times a week by sprinkling fresh grain moth eggs in excess. The tomato plants were also watered three times a week. The emerged adults were recorded every second or third day. Adult bugs were captured with an aspirator and their sex was determined. Altogether, pre-adult development was observed in 1726 individuals at 7 photothermal regimens (774 females and 952 males; no less than 99 individuals of either sex for each regimen).

Experiment No. 2: Assessment of the Influence of the Day Length on Maturation of Females of Dicyphus errans at 20°C

For this experiment we used the females reared under seven different photoperiodic regimens in experiment no. 1. After sex determination, adult bugs were placed in 250-ml glass containers (5–15 ind. in each, with a sex ratio of approximately 1 : 1) with tomato leaves (a cutting in moist sponge wrapped in plastic film) and kept at the same photoperiod at which they had been reared before the final molt. The group of

females placed in one container was treated as a cohort. The bugs were fed on grain moth eggs sprinkled in excess inside the container and onto the tomato leaves. As the leaves wilted they were replaced with fresh ones. The females were dissected 15 days after the final molt to determine their reproductive status: a female was considered to be reproductively active if its ovarioles contained at least one mature egg, and diapausing if no mature eggs were found. The eggs inside each reproductively active female were counted. Altogether, maturation of 651 females was observed under 7 photoperiodic regimens (6 replications and at least 78 females for each regimen).

Experiment No. 3: Assessment of the Influence of the Temperature on Adult Diapause Induction in Females of Dicyphus errans at a Near-Threshold Day Length

This experiment was carried out at two near-threshold photoperiods (14L : 10D and 15L : 9D) and two temperatures (20 and 25°C). The females were obtained in the same way as for experiment no. 2. The group of females placed in one container was considered a cohort. Altogether, maturation of 352 females was observed under 4 photothermal regimens (5 replications and at least 59 females for each regimen). Similar to experiment no. 2, the females were dissected 15 days after the final molt to determine their reproductive status.

Statistical Data Analysis

During data processing, a cohort of individuals was considered as an observation unit. For each cohort, the mean development time of individuals of either sex was determined in experiment no. 1, and the fraction of mature females, in experiments nos. 2 and 3. During analysis of the egg load, the data unit was a single female. Data were analyzed using ANOVA and Tukey's test. Nonparametric values (fractions) were transformed by the formula $Y = \arcsin\sqrt{x}$. All the calculations were performed using the SYSTAT 10.2 software package.

RESULTS

The effect of the day length on the pre-adult development time of males and females of *Dicyphus errans* at a temperature of 20°C. Two-way ANOVA of the whole body of data from experiment no. 1 (n = 83) showed that the duration of the pre-adult period of *D. errans* significantly depended on the photoperiod (F = 16.9, P < 0.001), and that females developed on average 1.3 days longer than males (F = 9.6, P = 0.003). The interaction of factors (sex and photoperiod) was statistically non-significant (F = 0.316, P = 0.927), i.e., the day length equally influenced the pre-adult development time of males and females. As can be seen in Fig. 1, the development time of both sexes was the shortest under short-day conditions (10–12 h of light a day), reached the maximum at 14 h, became somewhat (non-significantly) shorter at 15 h, and at 16 h (the longest of the tested photoperiods) it was the same as under short-day conditions.

The effect of the day length on maturation of females of *Dicyphus errans* at a temperature of 20°C. Experiment no. 2 showed that females of *D. errans* had a pronounced long-day photoperiodic response (PhPR) of adult diapause induction: under short-day conditions with day lengths from 10 to 14 h nearly all the females entered diapause, whereas under long-day conditions (15 and 16 h of light), about 90% of females were mature, i.e., reproductively active by the moment of dissection, on the 15th day after the final molt (Fig. 2*a*).

Mature females contained on average 6.3 ± 4.0 eggs (mean ± S.D.). As shown by ANOVA, this number did not depend on the photoperiod at which the female had been reared before and after the final molt (n = 190, F = 1.5, P = 0.188). It should be noted, however, that the dependence of the egg load on the photoperiod was difficult to determine because few mature females were recorded under short-day regimens.

The effect of the temperature on adult diapause induction in females of *Dicyphus errans* at a near-threshold day length. Two-way ANOVA of the whole body of data from experiment no. 3 (number of cohorts n = 20, Fig. 2*b*) showed that the percentage of mature females significantly depended on the photoperiod (F = 59.1, P < 0.001) but not on the temperature (F = 1.1, P = 0.301); the interaction of these factors was also statistically non-significant (F = 2.1, P = 0.164). As could be expected, the results obtained at 20°C in experiment no. 3 were practically identical to those of experiment no. 2 (compare Figs. 2*a* and 2*b*). The fraction of females that matured under the long-day conditions (14L : 10D) was twice as great at 25°C as at 20°C (Fig. 2*b*); however, according to one-way ANOVA, the difference was statistically non-significant due to extensive data scatter across the replications (n = 10, F = 2.8, P = 0.131).

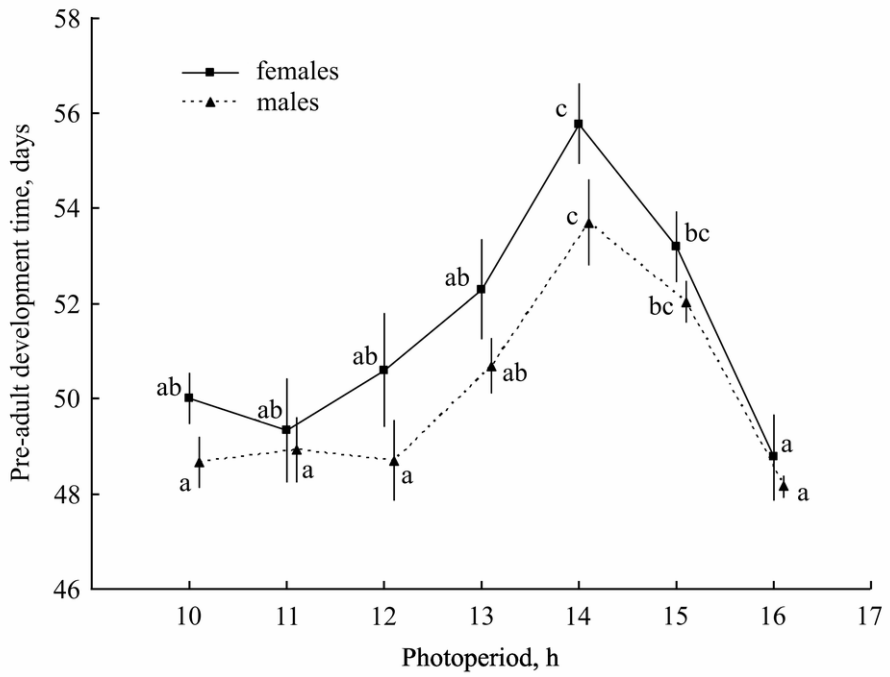

Fig. 1. The effect of the day length on the pre-adult development time of *Dicyphus errans* (Wolff) at 20°C (mean ± S.E.). The values marked with different letters on the same line are significantly different ($P < 0.05$; Tukey's test). The total number of individuals used in the experiment was $n = 774$ females and 952 males (no less than 99 ind. of either sex at each photothermal regimen).

DISCUSSION

Seasonal development of insects as a whole and true bugs in particular is controlled by a variety of ecological factors, of which the day length and temperature are the most important (Danilevsky, 1961; Danks, 1987; Musolin and Saulich, 2018). The eco-physiological responses to these external factors are strictly adapted to the local conditions and allow the populations of insects to optimize their seasonal development by using the warm season as fully as possible for feeding and reproduction and by entering winter diapause at the optimal time for prolonged winter physiological dormancy (Saulich and Volkovitsh, 2004).

Many taxa of insects have certain common features of seasonal development, such as voltinism, the form of seasonal polyphenism, and the prevalent type, form, and seasonal class of diapause (Vinogradova, 1991; Musolin, 2017; Saulich and Musolin, 2018). For example, the multivoltine seasonal cycle and embryonic diapause are considered to be the most common in plant bugs of the family Miridae (Wheeler, 2001; Saulich and Musolin, 2007). However, our model species *D. errans* makes an exception as it hibernates at the adult rather than at the egg stage (Voigt, 2005). Moreover, only females of this species appear to successfully overwinter in the nature (Wachmann et al., 2004), which is more typical of Anthocoridae than Miridae (Ruberson et al., 1998; Saulich and Musolin, 2009). Our laboratory experiments revealed a pronounced long-day PhPR controlling the induction of facultative adult diapause: nearly all the females entered diapause under short-day conditions (with photophases from 10 to 14 h inclusive), whereas under long-day ones (photophases 15 and 16 h) nearly 100% of females were reproductively active (Fig. 2*a*). The threshold of this PhPR was close to 14 h 30 min. The additional experiment no. 3 confirmed the long-day type of this PhPR and showed it to be thermostable: the shape of the response curve and the PhPR threshold were almost the same at two constant temperatures of 20 and 25°C (Fig. 2*b*). Thermostable PhPR of adult diapause induction is quite a rare phenomenon, and true bugs are generally characterized by thermolability of PhPR, manifested in a shift in its threshold or in changes in the general pattern of diapause induction depending on the temperature (Saulich and Volkovitsh, 2004; Saulich and Musolin, 2007).

Our experiments with *D. errans* revealed one more fairly distinct PhPR that was manifested at a different ontogenetic stage: the pre-adult development time of

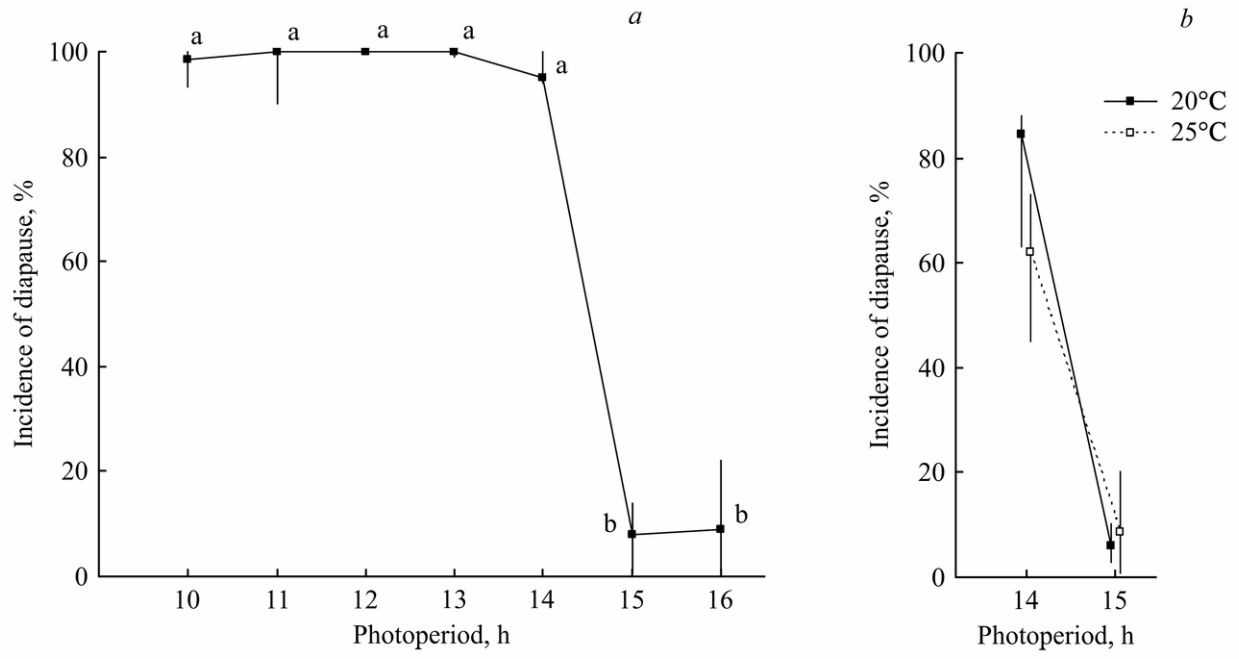

Fig. 2. The effect of the day length and temperature on adult diapause induction in females of *Dicyphus errans* (Wolff): (*a*) at 20°C (results of experiment no. 2); (*b*) at 20°C and 25°C (results of experiment no. 3). The data are presented as medians and quartiles in the series of replications. The number of cohorts was $n = 42$ (experiment no. 2) and $n = 20$ (experiment no. 3); the number of females was $n = 651$ (experiment no. 2) and $n = 352$ (experiment no. 3).

both males and females was controlled by the day length at which they were reared. Such a response to the day length is frequently observed in true bugs in the temperate zone and serves to optimize the phenological development of populations (Musolin and Saulich, 1997, 2007). Although the exact timing of hatching was not determined in our experiments, it may be quite confidently supposed that this PhPR was mostly manifested not in the eggs but in the nymphs.

The combination of two PhPR revealed in our experiments has an obvious adaptive significance. It is known that in Central Europe *D. errans* has multivoltine populations developing in 2 or 3 generations a year (Voigt, 2005) and hibernates as adults; it appears that only fertilized females actually live through winter while males perish as early as in autumn (Wachmann et al., 2004). Due to the thermostable PhPR, the timing of induction of winter adult diapause is always the same regardless of the weather conditions (temperature) in a particular year. In order to more precisely characterize the dynamics and seasonal timing of diapause induction in the nature, one has to determine the stage of development sensitive to the day length and to estimate the extent of short-day stimulation needed for diapause induction in females of *D. errans*. It would also be important to find out whether females that have already started laying eggs can stop reproducing and enter proper winter diapause in response to short-day conditions.

The periods of reproduction and pre-adult development of insects are often extended in time; individuals developing from early eggs usually have sufficient time to feed and prepare for hibernation, whereas nymphs hatching from later eggs may be unable to molt into adults in due time and enter stable winter diapause (Musolin and Numata, 2003, 2004). Under such conditions, the PhPR controlling the rate of pre-adult development has obvious adaptive significance: as the day length decreases in autumn to 10–12 h, the rate of nymphal development will increase even despite the seasonal drop of temperature, so that nymphs developing from later eggs will have better chances of reaching the adult stage and entering winter adult diapause (Musolin and Saulich, 1997; Saulich and Musolin, 2007).

The data of the above experiments should be taken into account when analyzing the seasonal development of *D. errans* and designing techniques for laboratory rearing of this species as a biological pest control agent. If the culture of *D. errans* is maintained under long-day conditions (e.g., 16L : 8D), its pre-adult de-

velopment will be relatively fast and the females will be reproductively active. Under short-day conditions (e.g., 12L : 12D) the pre-adult development will be equally fast but nearly all the females will enter diapause. At the near-threshold photoperiodic regimens (14L : 10D and 15L : 9D) pre-adult development will be slower while diapause induction may be unstable. However, it should be borne in mind that other geographic populations of *D. errans* may have some specific eco-physiological characteristics.

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