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Influence of Photoperiod on Development and Maturation of *Macrolophus pygmaeus* (Hemiptera, Miridae)

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Abstract—The effects of day length on development and reproductive maturation of zoophytophagous bug *Macrolophus pygmaeus* (= *M. nubilis*) were investigated under laboratory conditions using two strains originated from the environs of Rome, Italy (41.75°N, 12.30°E and 41.95°N., 12.80°E) and Sochi, Krasnodar Territory, Russia (43.9°N, 39.3°E). The insects were kept under day length of either 10 or 16 h at a constant temperature of 20°C. Nymphs and adults were fed on the grain moth eggs. Embryonic development lasted 18–20 days, nymphal development, 25–30 days, and reproductive maturation of females, 4–6 days. The short day length (10 h) resulted in 1–2-day prolongation of nymphal development and a longer maturation time in individuals from both strains, whereas the duration of embryo development was independent of photoperiod. Under both photoperiods, males developed faster than females. Under the short day length, females of the Rome strain matured markedly faster than those of the Sochi strain. Faster development under low temperature and stronger tendency to delay the reproductive maturation observed in the Sochi strain could be explained by a relatively fast (when compared with Rome) autumnal decrease in temperature. The mechanism and adaptive value of the long-day acceleration of development are not yet clear.

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It is well known that photoperiod (daylight time) can have a substantial impact on insect growth, development, and reproductive maturation. The patterns of photoperiodic responses are usually correlated with local climate and thus often show not only interspecific but also intraspecific (geographical) variation (Danilevsky, 1965; Tyshchenko, 1977; Tauber et al., 1986; Zaslavski, 1988; Chernyshev, 1996; Saulich, 1999; Denlinger, 2002; Saunders et al., 2002; Saulich and Volkovich, 2004). However, both the pattern and the range of intraspecific variability of seasonal adaptations substantially depend on the biological features of a given taxon. The studies conducted on different species of bugs (Hemiptera, Heteroptera) have demonstrated a wide geographical variation in different parameters of thermal and photoperiodic responses (Musolin and Saulich, 1997; Saulich and Musolin, 2007; Musolin and Ito, 2008; Pazyuk et al., 2014). These variations are often correlated with the peculiarities of the local climate. The range and pattern of this variability are essential prerequisites for successful adaptation to a new environment after occasional or intentional introduction outside the native range (Saulich, 1999; Boman et al., 2008; Facon et al., 2008; Musolin and Saulich, 2012).

The object of our study, the mirid bug *Macrolophus pygmaeus* Rambur (= *M. nubilis* H.-S.) (Hemiptera, Heteroptera, Miridae) is widely distributed over the Palaearctic region from Finland to Algeria and from the Faroe Islands to Turkmenistan and Tajikistan (Puchkov, 1978; Kerzhner and Josifov, 1999), although some modern authors believe that the records from Central Asia resulted from misidentifications (Martinez-Cascales et al., 2006; Sanchez et al., 2012).

Macrolophus pygmaeus, as well as the closely related *M. caliginosus* Wagner, is a zoophytophagous bug, i.e. it can feed not only on animals but also on plants (Perdikis and Lykouressis, 2000). That is why *Macrolophus* bugs can cause damage to cultivated plants. However, their beneficial effect on agrocenoses is much stronger than this minor damage and that is why *M. pygmaeus* is successfully used for biological control of thrips, aphids, spider mites, and some other pests in greenhouses and open fields (Boyarin, 2000; Krasavina et al., 2010; Messelink and Janssen, 2014;

Messelink et al., 2014). The data on its photoperiodic responses can be used for elaboration of the methods of mass rearing, storage, and application of this beneficial insect and thus our study can be of both fundamental and practical value.

It has been demonstrated that day length can have a significant impact on the feeding behavior of *M. caliginosus* and *M. pygmaeus* (Perdikis et al., 2004; Hamdan, 2006). The photoperiodic effects on duration of nymphal development and female maturation in *Macrolophus* species have not been studied in detail, whereas sporadic experiments have yielded ambiguous results (Hamdan, 2006), although namely it was these kinds of photoperiodic responses that were most often found in bugs (Tauber et al., 1986; Musolin and Saulich, 1997; Denlinger, 2002; Saunders et al., 2002; Saulich and Volkovich, 2004; Saulich and Musolin, 2007; Lundgren, 2011). We have investigated the influence of photoperiod on development and maturation of individuals from two laboratory strains of *Macrolophus pygmaeus* originated from bugs collected in Italy and on the Black Sea coast of Russia.

MATERIALS AND METHODS

The study was conducted with two laboratory strains of *Macrolophus pygmaeus.* "Rome strain" originated from 30–40 individuals collected in September 2013 in the environs of Rome, Italy from *Dittrichia viscosa* (L.) and *Solánum nígrum* L. in Ostia Antica (41.75°N, 12.30°E) and from *S. nigrum* and *Thýmus sp.* in Tivoli (41.95°N, 12.80°E). "Sochi strain" originated from 20 individuals collected from *Asarum* sp. in September 2011 in the environs of Sochi, Russia (43.9°N, 39.3°E). Before the study, both strains were reared in the Laboratory of Biological Control, All-Russian Institute of Plant Protection at a temperature of 24–27°C and day length of 16 h. Nymphs and adults were kept on tobacco *Nicotiana tabacum* L plants and fed on eggs of the grain moth *Sitotroga cerealella* (Oliv.), whiteflies *Trialeurodes vaporariorum* Westw., and flower pollen. The experiments were conducted in April-June 2014 in thermostatic chambers in the Laboratory of Experimental Entomology, Zoological Institute RAS.

To start the experiment, females of *M. pygmaeus* were randomly selected from the stock culture of both strains and released on tomato (*Solanum lycopersicum* L. variety Trans-Novinka) seedlings into 3.3 l plastic cages (3 plants and 20 females per cage). The females were fed on the grain moth eggs and kept at a temperature of 23±1ºC. In 24 h all the females were removed and the plants with the deposited eggs were randomly assigned to the two photoperiods (day lengths of 10 and 16 h) at a temperature of 20°C which is approximately equal to natural day length (including twilight) in November and in June at the latitudes of Rome and Sochi. The hatched nymphs of the 1st instar were collected daily and reared (10–20 nymphs per leaf) under the same conditions on tomato leaves placed in 250-ml transparent plastic containers covered with thin cotton tissue. The petioles of leaves were wrapped in wet cotton covered with a plastic foil. Food (the grain moth eggs) was provided every other day, tomato leaflets were replaced when necessary. The adult emergence was recorded daily; the adults were sexed, placed in groups (several males and females per group) and reared in the same containers under the same conditions. In 5 days after adult emergence, about half of females were dissected and the number of mature (chorionated) eggs in their ovaries was recorded. In 10 days after emergence, the rest of the females were dissected.

In total, data on development of 438 eggs and 326 nymphs (169 males and 157 females) were recorded and 153 females were dissected (80 females in 5 days after adult emergence and 73 females in 10 days after adult emergence). The sample size for each treatment of the experiment is indicated in the Results. Parametric data (the duration of development and the number of mature eggs) were analyzed with ANOVA; Student's t-test was used to compare treatments. The non-parametric data (the proportion of mature females) were compared with the χ^2 test. All calculations were made with SYSTAT 10.2. software.

RESULTS

Two-way ANOVA showed that the duration of *M. pygmaeus* eggs (embryo) development was independent of day length, whereas the difference between the populations was highly significant (Table 1). At both photoperiods, the development of eggs laid by females of the Sochi strain was 1.4–1.6 days (that is about 8%) shorter (Table 2). The same difference between the two strains was found in the duration of male larval development. In addition, male larvae developed slightly (2–4 %) faster under the long day conditions. Although in males of the Sochi strain this effect was somewhat stronger (Table 2) the interaction of the two factors was not significant (Table 1) sug-

Table 1. Influence of photoperiod and differences between populations on various biological parameters of *Macrolophus pygmaeus* (results of ANOVA)

Parameter and sample size (n)		Factor or interaction of factors (×)					
		photoperiod		difference between populations		photoperiod × difference between populations	
		F [1]	P [2]	F [1]	P [2]	F [1]	P [2]
Duration of development	eggs (n = 438)	0.13	0.719	221.09	< 0.001	1.52	0.218
	male nymphs (n = 169)	7.67	0.006	148.97	< 0.001	0.37	0.545
	female nymphs (n = 157)	31.3	< 0.001	1.66	0.199	1.87	0.172
The number of eggs in ovaries of mature females in relation to the time from the adult molt	in 5 days (n = 47)	1.93	0.174	0.17	0.682	1.09	0.303
	in 10 days (n = 67)	0.02	0.878	1.50	0.226	0.93	0.339

[1] Fisher's coefficient; [2] significance of influence

Table 2. Influence of photoperiod, inter-population differences, and differences between sexes on various biological parameters of *Macrolophus pygmaeus* (means and the results of the pairwise comparisons)

Day length, h		Population			
		Rome		Sochi	
		10	16	10	16
Duration of development, days ($X \pm SD$)	eggs	19.5 ± 1.2 a A n = 113	19.5 ± 1.1 a A n = 133	17.9 ± 0.9 a B n = 75	18.1 ± 0.9 a B n = 117
	male nymphs	27.8 ± 2.3 a A α n = 39	27.1 ± 2.6 a A α n = 63	26.0 ±1.8 a B α n = 24	24.9 ± 1.3 b B α n = 43
	female nymphs	29.4 ± 2.5 a A β n = 43	27.7 ± 2.7 b A α n = 44	29.4 ± 2.6 a A β n = 32	26.6 ± 2.3 b A β n = 38
The proportion of mature females in relation to the time from the adult molt	in 5 days	44 (22 – 66) a A n = 27	91 (65 – 99) b A n = 22	13 (0 – 43) a B n = 15	81 (48 – 96) b A n = 16
	in 10 days	92 (56 – 100) a A n = 13	100 (84 – 100) a A n = 26	79 (53 – 96) a A n = 14	90 (62 – 99) a A n = 20
The number of eggs in ovaries of mature females in relation to the time from the adult molt ($X \pm SD$)	in 5 days	4.0 ± 2.1 a A n = 12	4.4 ± 2.3 a A n = 20	2.5 ± 2.1 a A n = 2	5.0 ± 3.0 a A n = 13
	in 10 days	6.2 ± 3.8 a A n = 12	7.3 ± 3.9 a A n = 26	5.9 ± 3.6 a A n = 11	5.1 ± 3.8 a A n = 18

95% confidence intervals are given in brackets, values labeled with different letters are significantly different ($p < 0.05$, the Student's t-test): small Latin letters indicate the difference between the individuals of the same population which developed under different photoperiods, capital Latin letters indicate the difference between the individuals of different populations which developed under the same photoperiod, Greek letters indicate the difference between males and females of the same population which developed under the same photoperiod.

gesting that in the two studied strains the general pattern of this quantitative photoperiodic response was approximately the same. Female larvae of both strains under the long day developed 1.7–2.8 days (i.e., 6–10%) faster than under the short day, and, again, this long day acceleration of development was somewhat stronger in females of the Sochi strain (Table 2). Under both photoperiods, males of both strains developed faster than females, although in individuals of the Rome strain at a day length of 16 h this difference was statistically not significant.

The photoperiodic effect on the proportion of females that were mature (i.e. had at least one chorionated egg in the ovaries) on the 5th day after emergence was very strong: the percentages differed more than twice. This effect was also stronger in females of the Sochi strain and thus the difference between populations was significant only under the short day conditions (Table 2). However, on the 10th day after emergence, both the photoperiodic effect and the interstrain differences were weak and not statistically significant because practically all the females were mature. The number of chorionated eggs in the ovaries of mature females was very variable but did not significantly depend on photoperiod and on strain (Tables 1 and 2).

DISCUSSION

When differences in temperature are taken into account, the average duration of egg and nymph development of the studied strains agree with those obtained in previous studies on *M. pygmaeus* and *M. caliginosus* (Fauvel et al., 1987; Hart et al., 2002; Hamdan, 2006; Castañé and Zapata, 2005; Castañé et al., 2007; Mollá et al., 2014). Protandry (the faster development of males) is typical of many insects and, in particular, it was reported for *M. caliginosus* (Hart et al., 2002; Castañé and Zapata, 2005).

Short-day conditions often speed up pre-adult development of temperate insects (Danilevsky, 1965; Tyshchenko, 1977; Tauber et al., 1986; Zaslavski, 1988; Chernyshev, 1996; Denlinger, 2002; Saulich and Volkovich, 2004) including some bugs (Musolin and Saulich 1997; Saulich and Musolin, 2007; Lopatina et al., 2007; Musolin and Ito, 2008) while *M. pygmaeus* shows the opposite pattern of reaction. Possibly, the reason is that the potential adaptive value of the short-day acceleration of development is to increase the fraction of individuals that reach the overwintering stage, whereas *M. pygmaeus* in natural conditions reportedly overwinter mostly as nymphs of various ages (Puchkov, 1978). Open field overwintering experiments with *M. caliginosus* also suggested that nymphs survived longer than adults (Hart et al., 2002). A laboratory study conducted by Hamdan (2006) did not find any significant difference between nymphal development time of *M. caliginosus* under short (8 h) and long (16 h) day conditions. Disagreement with the results of our study can be explained not only by interspecific differences but also a small sample size and very high variability of the results: the photoperiodic effect in *M. caliginosus* was only marginally insignificant ($P = 0.094$).

Acceleration of development under the long day conditions was rarely reported for bugs (Musolin and Saulich 1997; Saulich and Musolin, 2007), although it was observed in two stink bug species: *Dolycoris baccarum* L. (Conradi-Larsen and Sømme, 1973) and *Nezara viridula* L. (Ali and Ewiess, 1977). It should be noted that the first authors (Conradi-Larsen and Sømme, 1973) used a 8 h day as a "short day treatment" that is not "ecologically relevant" in Norway. In the second case, the authors (Ali and Ewiess, 1977) stated that the effect can be explained by the fact that the increase in day length caused an increase in the duration of daily feeding period and corresponding acceleration of the rate of nymphal growth and development. Moreover, the studies conducted with other populations of the same species demonstrated an "autumnal" acceleration of development under combination of low temperature and short day conditions and a deceleration of development under the threshold photoperiods that is typical of other Hemiptera species (Musolin and Numata, 2003; Nakamura, 2003; Saulich and Musolin, 2007).

It is well known that short photoperiods often induce a winter reproductive diapause (Danilevsky, 1965; Tyshchenko, 1977; Tauber et al., 1986; Zaslavski, 1988; Chernyshev, 1996; Denlinger, 2002; Saunders et al., 2002; Saulich and Volkovich, 2004). In particular, the long day photoperiodic response was observed in many bug species (Musolin and Saulich, 1997; Musolin and Numata, 2003; Musolin et al., 2004; Gillespie and Quiring, 2005; Saulich and Musolin, 2007; Musolin and Ito, 2008; Brent and Spurgeon, 2011; Lundgren, 2011). However, in *M. pygmaeus* the effect of short day (at least at a temperature of 20°C which was used in our experiments) was manifested merely as a short-term delay in reproductive maturation: on the 10th day after emergence, practically all females matured. The number of mature (chorionated) eggs found in the ovaries of ovipositing females was not dependent on day length which can be possibly explained by the fact that eggs are laid as they mature. The earlier study conducted with *M. caliginosus* yielded similar results (Castañé et al., 2007).

Although Rome and Sochi are located at almost the same latitude these two cities have different climates: the yearly average temperatures are 15.9 and 14.6°C, correspondingly. The difference in the rate of the autumnal drop in temperature is even larger: the mean temperatures of September, October, November, and December in Rome are 20.7, 17.7, 13.4, and 9.8°C, whereas in Sochi they are 20.9, 16.5, 11.6, and 7.6°C (data from the cite http://www.weatheronline.co.uk). Insect populations inhabiting colder environments often show a relatively high rate of development at low temperatures and a stronger tendency to enter diapause or to delay reproductive maturation under short day conditions (Danilevsky, 1965; Tyshchenko, 1977; Tauber et al., 1986; Zaslavski, 1988; Chernyshev, 1996; Honek, 1996; Saunders et al., 2002; Lopatina et al., 2007; Musolin and Ito, 2008; Pazyuk et al., 2014). It was these differences between Rome and Sochi populations of *M. pygmaeus* that we have found.

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