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Photoperiodic Control of Nymphal Growth in True Bugs (Heteroptera)

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Abstract—The photoperiodically induced retardation of nymphal growth in 11 species of terrestrial true bugs (Pentatomidae, Pyrrhocoridae, Coreidae, and Alydidae) is considered as quantitative photoperiodic response and analyzed in detail on the basis of original and previously published experimental data. Eight species showed growth delays under long day conditions. These delays were 10-20% for *Arma custos, Graphosoma lineatum, Eurydema oleracea, Eysarcoris lewisi, Coreus marginatus*, 30–40% for *Palomena prasina,* and 50–60% for *Palomena angulosa, Pyrrhocoris apterus*. In *Carbula humerigera, Nezara viridula,* and *Dolycoris baccarum* this effect was registered under short day conditions. However, photoperiodic conditions do not control nymphal growth rates in *Picromerus bidens, Alydus calcaratus, Riptortus clavatus,* and *Podisus maculiventris.* Various aspects of the phenomenon are analyzed. The ecological significance of this photoperiodic response for control of life cycles in uni- and polyvoltine bug species is discussed.

All photoperiodic phenomena are usually classified into two categories: qualitative and quantitative responses. The origin and mechanisms of these two types of responses have not yet received a unified and widely accepted interpretation (Zaslavskii, 1975, 1984; Tyshchenko, 1976, 1977, 1981). It is clear, however, that qualitative photoperiodic response (PhPR) changes the direction of morphogenetic processes and determines the course of development, while quantitative photoperiodic response controls growth processes and morphometric features, and regulates the intensity of biological and physiological processes without changing their direction (Tyshchenko, 1981; Tauber *et al*., 1986; Danks, 1987; Numata and Kobayashi, 1989).

Qualitative photoperiodic responses (induction and termination of diapause, seasonal polymorphism and aphid cyclomorphosis must be mentioned as the most important) have been much studied in many insect species. Quantitative responses are less well known, though even a brief list of examples (Table 1) shows that these responses are widely spread among insect species, being very diverse.

Quantitative responses controlling rates of growth play an important role in the regulation of the seasonal cycles in insects. Photoperiodic control of growth rates has been recorded in representatives of both Hemimetabola and Holometabola. Danks (1987) gives a list of 80 species from 37 families and 9 of the biggest insect orders in which this kind of environmental control of development is known. It should be mentioned that in each order there are species whose nymphal development is accelerated by long day and retarded by short day, and species characterized by opposite responses. Perhaps, the only exception in this list is the section “Hemiptera” (Heteroptera-Homoptera): only examples of long-day growth acceleration are mentioned here (except *Pyrrhocoris apterus* with reference to Saunders, 1983).

By now, much more heteropteran species with photoperiodic control of nymphal growth have been studied. However, experimental evidence is scattered in separate papers and has never been analyzed in the aggregate. Different durations of nymphal development were recorded in some of our experiments as well. That is why it turned out necessary to consider the whole set of data and conduct a comparative ecological analysis of the available information, and just this was done in this paper.

The experimental part of the research was performed at the Les na Vorskle Reserve (Forest on the River Vorskla) in forest-steppe zone of Russia, 50°N.

Bugs from three heteropteran families were used in the experiments: Pentatomidae—*Arma custos* F., *Graphosoma lineatum* L., and *Palomena prasina* L., Pyrrhocoridae—*Pyrrhocoris apterus* L., Coreidae—*Coreus marginatus* L.

Table 1. Examples of photoperiodic control of quantitative characters in insects

Quantitative character	Insect species	Reference
Duration and intensity of diapause	*Spilarctia imparilis*	Kimura *et al*., 1982
	Oedipoda miniata	Pener and Orshan, 1980
	Teleogryllus emma	Masaki, 1965, 1972
	Luehdorfia japonica	Ishii and Hidaka, 1982
	Riptortus clavatus	Numata and Hidaka, 1983
	Calliphora vicina	Vinogradova, 1978, 1991
	Chrysoperla downesi	Tauber M. and Tauber C., 1975
	Chrysopa carnea	Tauber *et al*., 1986
Weight of pupae	*Barathra brassicae*	Tyshchenko and Gasanov, 1983
	Acronycta rumicis	
	Pieris brassicae	
Rates of female maturation	*Chrysopa carnea*	Volkovich, 1987
Sizes and body proportions	*Euscelis incisus*	Müller, 1957, 1979
	Stenocranus minutus	Nakasuji *et al*., 1984
	Parnara guttata	
Duration (rates) of nymphal development (sometimes with additional instars)	*Hadena sordida*	Bobinskaya, 1966
	Agrotis occulta	Danilevskii, 1961
	A. segetum	Geispits *et al*., 1971
	Dasychira pudibunda	Geispits and Zarankina, 1963
	Teleogryllus emma	Masaki, 1972
	T. yezoemma	
	Pterostichus oblongopunctatus	Schaick, 1985
	Pyrrharctia isabella	Goettel and Philogene, 1978
	Pteronemobius nitidus	Tanaka, 1983
	Melanoplus sanguinipes	Dean, 1982
Nymphal body coloration	*Arma custos*	Volkovich and Saulich, 1994
	Plautia stali	Numata and Kobayashi, 1994
Pupae coloration	*Orgyia thyellina*	Kimura and Masaki, 1977
Adult body coloration	*Riptortus clavatus*	Kobayashi and Numata, 1993, 1995
Fecundity	*Plutella maculipennis*	Atwal, 1955 and Harcourt and Ñass, 1966
	Platycleis grisea	Helfert, 1980
	Phaneroptera nana	
	Locusta migratoria	Perez *et al*., 1971
	Teleogryllus spp.	Masaki, 1972
Sexual behavior	*Locusta migratoria*	Perez *et al*., 1971
Sex ratio	*Compoletus perdistinctus*	Hoelscher and Vinson, 1971
Ovarian development	*Acrolepia assectella*	Meudec, 1966
Recovery from heat stress	*Drosophila melanogaster*	Pittendrigh, 1961—after Saunders, 1976

Table 2. Duration of nymphal development

Species	Number of generation in the region	Temperature conditions, °C	Duration of development*						Reference
			min			max			
			PhP, h	days, M±m	%	PhP, h	days, M±m	%	
Polyvoltine species									
Arma custos	1	Laboratory thermorhythm 26.8 : 13.5	12	41.1±0.57	100.0	17	48.9±0.61	119.0	Volkovich and Saulich, 1994
		Natural thermorhythm 17.2 (23.3 : 12.7)	14	58.2±0.74	100.0	18	69.7±1.18	119.8	ibid.
Graphosoma lineatum	1	Constant, 24	17	27.1±0.21	100.0	19	32.1±0.87	118.5	Musolin and Saulich, 1995
Eurydemaole racea	1–2	Constant, 20	14	39.4	100.0	20	47.2	119.8	Fasulaty, 1976
Eysarcoris lewisi	2	Laboratory thermorhythm, 27 : 23	12	24.2±0.18	100.0	16	28.8±0.29	119.0	Hori, 1991, from L_{II} to L_{V}
Pyrrhocoris apterus	1–2	Constant, 20	15	52.7±0.20	100.0	17	79.0±0.97	149.9	Saulich *et al.*, 1993
		Constant, 24	14	36.0±0.26	100.0	16	40.2±0.57	111.7	Saulich, Volkovich and Numata, unpubl.
		Laboratory thermorhythm, 27 : 13	12	39.0±0.21	100.0	18	54.3±0.45	139.2	ibid.
		Laboratory thermorhythm, 27 : 33	12	29.7±0.14	100.0	17	36.9±0.33	124.2	ibid.
		Natural thermorhythm, 1990 17.2 (23.3 : 12.6)	14	68.3±0.55	100.0	17	75.7±1.08	110.8	ibid.
		Natural thermorhythm, 1991 19.9 (25.7 : 15.1)	16	48.0±0.40	100.0	18	53.9±0.58	112.3	ibid.
Monovoltine species									
Coreus marginatus	1	Natural thermorhythm 20.6 (29.0:13.5)	15	43.7±0.26	100	18	48.8±2.58	111.7	Musolin, unpubl.
Palomena prasina	1	Constant, 20	15	48.8±0.56	100.0	18	65.2±1.99	133.6	Saulich, unpubl.
		Constant, 26	15	40.6±1.50	100.0	17	46.7±1.22	115.0	ibid.
						18	46.7±1.67	″	ibid.
		Constant, 30	15	34.6±1.17	100.0	17	38.9±0.80	113.5	ibid.
Palomena angulosa	1	Laboratory thermorhythm, 27 : 33	12	42.03	100.0	15	65.75	156.4	Hori, 1988, with L_{I}
Carbula humerigera	1	Constant, 25	0	50.6±3.7	100.0	13	99.7±13.7	196.8	Kiritani, 1985b

* Values of the duration of nymphal development are compared using the *t*-test. Confidence level is 99.9%, with an exception of the experiment with *C. marginatus* (95.0%).

** All polyvoltine species have a PhPR of long-day type.

Quantitative photoperiodic effects were studied at constant and fluctuating temperatures under laboratory conditions and under natural daily temperature fluctuations outdoors.

In the laboratory experiments, insects were reared in photothermostatic chambers (Braun and Goryshin, 1978). The light intensity in the chambers ranged between 180 and 250 Lx (fluorescent lamps, 20 W). In the chambers constant photoperiod (PhP) and temperature were maintained automatically. In some experiments, thermorhythmical conditions were applied, and experimental insects were transferred manually from one temperature regime to another every morning and evening. In such a manner a 12-hour rhythm was created, the cold period of which was coincided with the scotophase, while its warm period combined with the photophase of the photoperiodic cycle. Since duration of the photophase exceeded 12 h in all the experimental regimes, and cold component of the daily cycle overlapped with the beginning of the photophase.

In the field experiments, insects were reared under constant PhP and natural daily rhythm of temperature. Photoperiodic conditions were maintained by a special semi-automatic device (Braun and Goryshin, 1984).

The deviation from the set temperature was not more than 1.0°C. In the field experiments, the ambient temperature was recorded by a daily thermograph and checked by thermometers.

The methods of laboratory rearing of *A. custos, G. lineatum,* and *P. apterus* have been described in detail previously (Numata *et al.*, 1993; Volkovich *et al.*, 1994; Musolin and Saulich, 1995; Saulich *et al.*, 1995). This is why only methods of rearing of other species are given here.

Lilac (*Syringa vulgaris*) leaves and Siberian pea shrub (*Caragana arborescens*) pods served as food for the nymphs of *P. prasina*. The insects were reared in plastic Petri dishes 100 mm in diameter, with lids having 50-mm diameter openings for aeration, covered with gauze. Each egg-batch was placed in a separate Petri dish. While nymphs grew, their density was reduced to 5–6 individuals per Petri dish by the 5th instar. The appearance of adults was registered daily.

C. marginatus nymphs were reared using a similar procedure. Younger instar nymphs were fed on tancy (*Tanaceum sp*.) sprouts and common burdock (*Arctium lappa*) leaves; to the diet of elder instar nymphs were added leaves and, on becoming available in the nature, also generative parts of horse sorrel (*Rumex confertus*).

To conduct a more detailed analysis of the role photoperiodic conditions play in nymphal growth of heteropterans, we considered not only original, but also previously published data on pre-imaginal development of other bug species. The temperature and photoperiodic conditions of these experiments are briefly described in Table 2 and in the legends of the corresponding figures. The schemes of these experiments differed slightly, but this created no obstacles to revealing the common features.

Retardation of Nymphal Growth under Long-day Conditions

A. custos. Changes of duration in the pre-imaginal development were most pronounced under changing temperature conditions in the laboratory and field experiments, with the highest values achieved in the field. The duration of nymphal stage gradually increased from 58.2 days at a PhP of 14 h (the shortest one from the photoperiods tested in the experiments) to 69.7 days at a PhP of 18 h (the longest one). The difference between these two values amounted to 20%. In the experiments with laboratory thermorhythms, a strong tendency for the pre-imaginal development to be prolonged was observed as well (curve *2*; Fig. 1). Under a constant temperature of 27°C, this tendency was not observed, and fluctuations of the duration of nymphal stage ranged from + 1.2 to 12.1%, as compared with the shortest value (Volkovich and Saulich, 1994).

G. lineatum. The duration of nymphal development was about the same for photoperiodic regimes between 15 and 17 h, though at a longer photophase (18 and 19 h) this duration gradually increased (14.6 and 18.5% respectively). This trend was only observed under a constant temperature of 24°C (Fig. 2); at 28°C, the difference was insignificant (Musolin and Saulich, 1995).

Eurydema oleracea (Pentatomidae). As well as in the previous species, in this bug, retardation of nymphal development (19.8%) was only observed at a lower temperature of 20°C, but not at 25°C (Fasulati, 1976).

Eysarcoris lewisi (Pentatomidae). The response of this species was studied under laboratory thermorhythm (27 : 23°C) and three PhPs (Hori and Ina-

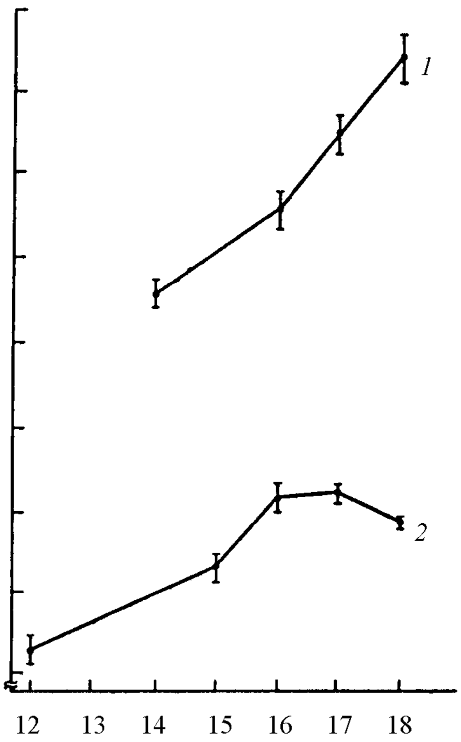

Fig. 1. Nymphal development of *Arma custos*: *1*—natural thermorhythm, 17.2°C (23.3 : 12.7°C); *2*—laboratory thermorhythm, 20.2°C (26.8 : 13.5°C) (data from Volkovich and Saulich, 1994). *Abscissa*—photoperiod, h; *ordinate*—duration of nymphal development, days. *Vertical bars* shows standard error.

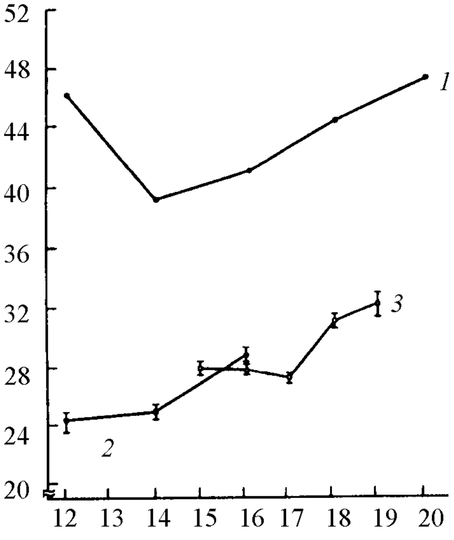

Fig. 2. Nymphal development of: *1*—*Eurydema oleracea,* 20°C (data from Fasulati, 1976); *2*—*Eysarcoris lewisi,* laboratory thermorhythm, 27 : 23°C (data from Hori, 1991, without the 1st nymphal instar); *3*—*Graphosoma lineatum,* 24°C (data from Musolin and Saulich, 1995). *Abscissa*—photoperiod, h; *ordinate*—duration of nymphal development, days. *Vertical bars* shows standard error.

mura, 1991). Unfortunately, the duration of the 1st nymphal instar stage was not indicated in the original paper, and it is only possible to state that the period from the 1st nymphal ecdysis to the appearance of adults was 102% at PhP of 14 h and 119% at PhP of 16 h, as compared with the duration of the development under short-day conditions of 12 h (Fig. 2).

P. apterus. This species was investigated in more detail (Fig. 3). In the laboratory experiments, nymphal development was studied under three constant temperature regimes (20, 24 and 27°C), with day-length in the range from 14 to 18 h. In all regimes, the duration of pre-imaginal development decreased with increasing temperature. While analyzing the influence of photoperiodic conditions on nymphal growth, it should be mentioned that there was a well pronounced “peak” (the maximum retardation of growth) in the critical, or near-threshold zone at 20°C. Sounders was the first to describe this phenomenon in this species’ population from Central Bohemia (1983). In his experiments, the photoperiodic threshold of diapause induction was 15 h 45 min, while a “peak” was recorded at 16 h 30 min (at 25°C). In the Belgorod population of this species, the “peak” was recorded at 20 and 24°C (Numata *et al*., 1993; Saulich *et al*., 1993) and could not be observed at higher temperature (27^{o}C). In general, the quantitative response was weaker in this species at higher temperatures. Rise in temperature simultaneously reduced the photoperiodic threshold of diapause induction (Numata *et al*., 1993; Saulich *et al*., 1994).

Under conditions of laboratory thermorhythm (27 : 13, 33 : 13, and 33 : 20°C with average temperatures of the rhythms 20, 23, and 26°C respectively), the retardation of nymphal growth was also the most pronounced at the lowest temperatures (27 : 13°C). When extreme values are considered, it should be mentioned that nymphs developed 15 days (39.2%) longer under long-day conditions (18 h) than under short-day conditions (12 h).

At a thermorhythm 33 : 13°C, the most pronounced retardation of nymphal growth was recorded at PhP of 17 h (124.2%). In a set of experiments with an average temperature of 26°C, there were no long-day retardations of nymphal growth.

Under constant PhP and natural daily fluctuations of temperature, this tendency was weak, and only distinct in an experiment carried out in 1990 (Fig. 3c) when the retardation under long-day conditions (18 h) amounted to 10.8%.

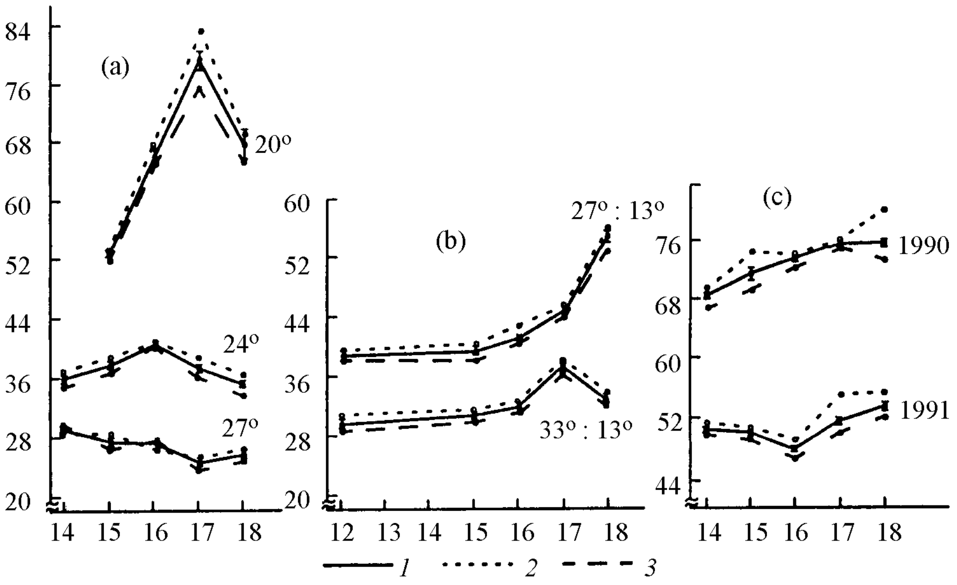

Fig. 3. Nymphal development of *Pyrrhocoris apterus*: (a) constant temperature, (b) laboratory thermorhythm, (c) natural thermorhythm. Duration of development: *1*—mean for all nymphs, *2*—mean for males, *3*—mean for females. *Abscissa*—photoperiod, h; *ordinate*—duration of nymphal development, days. *Vertical bars* shows standard error.

C. marginatus. Under conditions of natural daily thermorhythm, the duration of pre-imaginal development in this species gradually increased with day-length increasing from 15 h (100%) to 18 h (112%), but again decreased at 19 h (105%). In this experiment no qualitative PhPR was revealed: all adults were determined to diapause and did not begin reproduction.

P. prasina. At 20°C, at constant PhPs in the range from 15 h to 18 h, each 1-hour increase of day-length resulted in an approximately 10% retardation of the duration of nymphal development. As a result, nymphs grew 1.34 times longer under 18 h photoperiodic conditions, as compared with the 15 h. This tendency was less pronounced at 26°C, and absolutely disappeared at 30°C (Fig. 4). It should be mentioned that neither short nor long-day conditions induced reproduction, and diapause was recorded in all regimes.

Palomena angulosa (Pentatomidae). This species was studied under laboratory thermorhythm (27°C 8 h and 23°C 16 h) and three constant PhPs (12, 14, and 15 h) (Hori, 1988). The growth duration of nymphs of the species was 40% longer at a PhP of 14 h and 56% longer at PhP of 15 h as compared with the 12 h regime. It should be noted that Hori reported only the development duration of nymphal instars from 2nd to

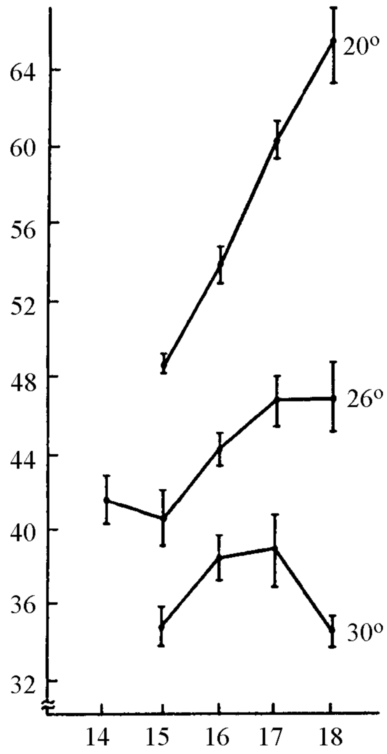

Fig. 4. Nymphal development of *Palomena prasina. Abscissa*—photoperiod, h; *ordinate*—duration of nymphal development, days. *Vertical bars* shows standard error.

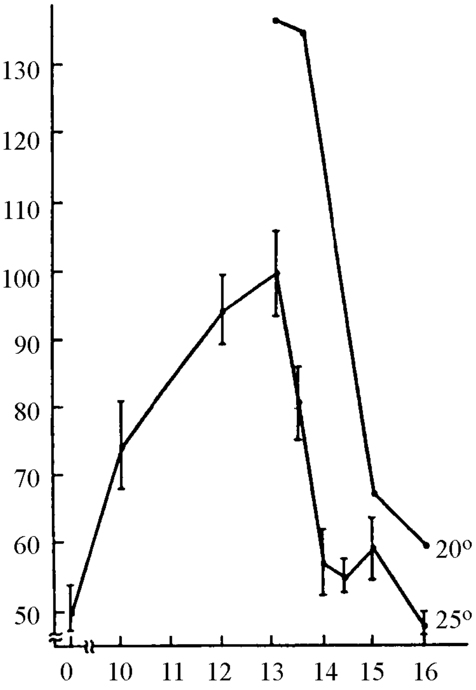

Fig. 5. Nymphal development of *Carbula humerigera* (data from Kiritani, 1985). *Abscissa*—photoperiod, h; *ordinate*—duration of nymphal development, days. *Vertical bars* shows standard error.

5th; duration of growth of 1st instar nymphs is taken on the basis of indirect data (Hori, 1987, 1988). In Hori's opinion, there is a linear relationship between the duration of nymphal development and PhP, and this relationship can be expressed by linear regression equation under conditions of either constant or decreasing day-length (Hori, 1987, 1988).

Carbula humerigera (Pentatomidae). The quantitative PhPR of this species turned out to be very peculiar. At 25°C, the duration of nymphal stage gradually increased with the PhP increasing from 0 h (100%) to 13 h (197%), and after that decreased when the PhP increasing further to 16 h (Fig. 5) (Kiritani, 1985b). The same tendency showed at a lower temperature of 20°C. A total of ten PhPs (from 0 to 16 h) were studied at 25°C, and five PhPs (from 13 to 16 h), at 20°C.

Short-Day Retardation of Nymphal Development

While analyzing the influence of photoperiodic conditions on the nymphal growth, Hori (1986) pointed out that the majority of the studied heteropterans can be classified as species of long-day type acceleration. He placed in this group *Dolycoris baccarum, Nezara viridula,* and *Carbula humerigera*.

D. baccarum (Pentatomidae) was studied under two PhPs (8 and 16 h) at a temperature of 21°C (Conradi-Larsen and Sømme, 1973). Under short-day conditions, the complete nymphal development took 3.8 days longer (9.5%) than that under long-day conditions; this difference being statistically reliable. However, when duration of separate nymphal instars are compared, it is found that significant differences are only observed for the 2nd ($P < 0.05$) and 3rd ($P < 0.01$) instars.

Another bug species mentioned by Hori, *N. viridula*, had been studied in detail by Ali and Ewiess (1977). Retardation of nymphal development was recorded under short-day conditions at three temperature regimes, and this tendency was regular and well pronounced at 25°C (Fig. 6). The authors suggested that the longer photophase ensured a longer period suitable for nymphal feedings, which resulted in an intensification of metabolism and acceleration of the whole nymphal development.

Bug Species in which no Photoperiodic Control of Nymphal Growth Was Found

The examples considered above demonstrate that many heteropteran species show quantitative PhPR which induces retardation of nymphal growth, and this retardation may be associated with either long- or short-day conditions. At the same time, there are bug species in which the duration of nymphal development is not controlled by PhP. For example, no regular relationship between the duration of nymphal development and PhP has ever been recorded in *Podisus maculiventris* Say (Pentatomidae), a predatory bug introduced from the U.S., reared under various photoperiodic and temperature regimes (Goryshin *et al.*, 1988). Similar results were obtained in our experiments with three other heteropteran species: *Picromerus bidens* L. (Pentatomidae) (Musolin, 1996), *Alydus calcaratus* L., and *Riptortus clavatus* Thunberg (Alydidae) (unpubl. data).

Nymphal Diapause of Carbula humerigera as an Extreme Example of the Photoperiodically Induced Growth Retardation

Experiments carried out by Kiritani (1985b) demonstrated that at a temperature of 25°C, nymphal development of this species lasts twice as long at a PhP of 13 h than at a PhP of 16 h or in constant darkness. A 30–40-day retardation of nymphal growth under short-day conditions was considered a facultative nymphal winter diapause. The earlier in the season nymphs hatch out, the higher the instar at which nymphs enter the diapause. After overwintering nymphs molt to an imaginal stage at the beginning of the next summer.

Photoperiodically Induced Retardation and Nymphal Age

In analyzing the age arrangement of photoperiodically induced retardation, the results of the experiments with *P. prasina, P. angulosa,* and *E. lewisi* were taken into consideration.

The duration of nymphal development of *P. prasina* is shown in Fig. 7a and expressed in per cent, with the duration under the shortest-day conditions (PhP of 15 h) taken to be 100%. This way of data presentation allows one not only to show the long-day retardation, but also to reveal the instar(s) in which this retardation is the most significant. It is easy to see that the influence of PhP on the duration of nymphal growth is not pronounced in 1st and 2nd instars. This tendency remains weak during the 3rd instar, but becomes highly pronounced during the last two instars.

A similar pattern was observed in two other species, *P. angulosa* (Fig. 7b) and *E. lewisi* (Fig. 7c), with the retardation highly pronounced even in the 3rd nymphal instar (interpretation of data of Hori, 1988; Hori and Inamura, 1991).

The last (5th) nymphal instar was the longest stage of the pre-imaginal development in all the species considered: it accounted for approximately one third of the whole period of nymphal development. The most significant part of the photoperiodically induced retardation took place during this particular instar.

Differences between Sexes

It is well known that in some insect species the duration of pre-imaginal development differs between sexes. For example, in some species, adult females mature before males, in other species, an opposite tendency can usually be observed. This phenomenon known as protandry and protogyny, is especially pronounced and well understood in parasitic hymenopterans (Victorov, 1976).

The available data allow us to reveal, how this biological feature of the species manifests itself in heteropterans under different photoperiodic conditions.

The most comprehensive data for such kind of analysis was obtained in experiments with *P. apterus.* In 32 of 34 regimes (Fig. 3), females completed their nymphal development earlier than males. This was observed both at constant temperatures (20 and 24°C; Fig. 3a) and under laboratory or natural thermorhythms (Figs. 3b and 3c). It should be mentioned that at a constant temperature of 20°C, the "peak" in the threshold zone, discussed earlier, was highly pronounced in both sexes (Fig. 3a) with the differences in nymphal development duration between sexes being the greatest (7.3 days) under this regime.

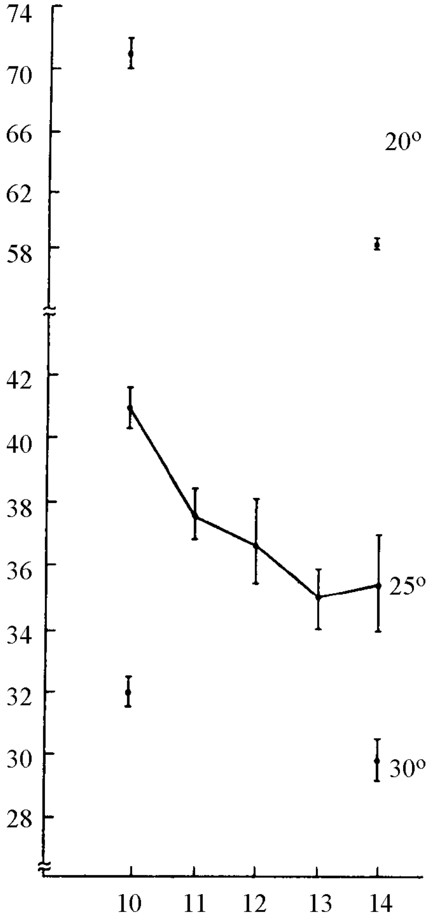

Fig. 6. Nymphal development of *Nezara viridula* (data from Ali and Ewiess, 1977). *Abscissa*—photoperiod, h; *ordinate*—duration of nymphal development, days. *Vertical bars* shows standard error.

An opposite pattern, namely faster development of males, was observed in this species only twice: at constant temperature of 27°C and PhPs of 14 and 16 h. As mentioned above, at this temperature the quantitative PhPR did not manifest itself at all.

In the experiments with *G. lineatum* and *C. marginatus,* no clear difference was observed between the duration of nymphs in the two different sexes.

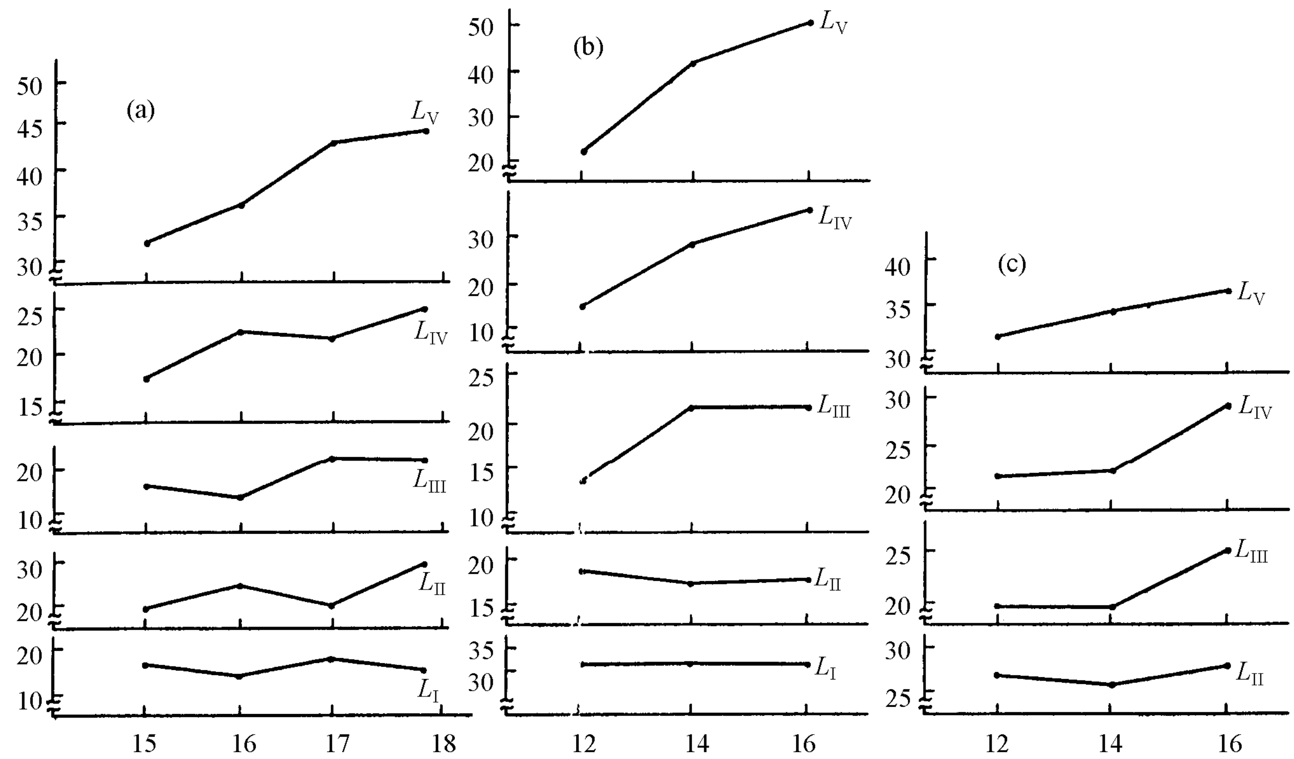

Fig. 7. Duration of separate nymphal instars: (a) *Palomena prasina,* 20°C (100%—whole nymphal development at PhP of 15 h); (b) *Palomena angulosa,* laboratory thermorhythm, 27 : 23°C (data from Hori, 1988, modified; 100%—whole nymphal development at PhP of 12 h); (c) *Eysarcoris lewisi,* laboratory thermorhythm, 27 : 23°C (data from Hori, 1991; 100%—nymphal development from L_{II} to L_V at PhP of 12 h). L_I—L_V—nymphal instars. *Abscissa*—photoperiod, h; *ordinate*—duration of each nymphal instar, %.

Maintaining a species-specific feature, namely a faster development of nymphs of one particular sex, is one of important biological properties of quantitative PhPR. This indirectly proves that, firstly, retardations of nymphal growth are not accidental, and, secondly, day-length does not disrupt other physiological processes while controlling rates of nymphal development.

The Influence of Higher Temperatures

Any physiological response has its own temperature optimum and limits of manifestation. Quantitative PhPR is no exception to this rule.

As it was repeatedly mentioned above, at higher temperatures the retardation of growth was significantly weaker, or often completely disappeared. At constant temperature, it was observed in *G. lineatum, E. oleracea, P. apterus,* and *P. prasina.* Under conditions of laboratory thermorhythms, increasing the average temperature of the rhythm suppressed this response in *P. apterus.*

No examples of an alternative response to higher temperatures (naturally in the range of favorable temperatures) were found.

The Role of Changing Day-Length

In nature, insects develop under conditions of seasonal changes of day-length (increasing day length during the 1st part of the vegetative season, and a decreasing day length during its 2nd part), rather then under conditions of constant PhP.

Experimentally, conditions of changing day-length can be created either by a single change of one constant PhP to an alternative one, or by gradual (for example, daily) decrease or increase of day-length by a certain interval of time.

Experiments of this kind are seldom. According to the available data, among terrestrial heteropterans, the influence of changing day-length has only been studied in *C. humerigera* (Kiritani, 1985b) and *P. angulosa* (Hori, 1986, 1987).

In the experiments with *C. humerigera,* nymphs at different stages of development were transferred once from the conditions of constant PhP of 10 or 12 h to the conditions of constant PhP of 12, 13 or 14 h. It was found that this increase in day-length was more effective in synchronization of adult emergence rather than in acceleration of nymphal development (Kiritani, 1985b, p. 262).

In *P. angulosa*, constant long day (PhP of 16 h) retarded growth with a significant variation, also resulting increased mortality. A regularly decreasing PhP accelerated nymphal development. The shorter the PhP at which nymphs were reared, the more significantly was their development accelerated (see above; Hori, 1987).

Unfortunately, experiments with *C. humerigera* and *P. angulosa* were carried out according to different procedures. As a consequence, the responses of these two species to changing day-length cannot be compared in detail.

The Ecological Significance of Photoperiodically Induced Retardation of Nymphal Development

The species as a whole and its particular local population, develop a complex of seasonal adaptations aimed at establishing a more effective correspondence between the insect's seasonal cycle and the environmental conditions. The photoperiodically induced retardations of nymphal development can be considered adaptations of this kind as well.

The Polyvoltine Species

The photoperiodic control of the duration of nymphal development allows polyvoltine species to use to the greatest possible extent the temperature and food resources of the region, which is achieved by producing the maximum number of generations during the vegetative season.

P. apterus. It was established that in the forest-steppe zone (50°N) this species can produce one or two generations (Saulich *et al*., 1993; Saulich *et al*., 1994). One generation per year is a seasonal pattern by which develop the bugs hatching from the late egg-batches or the whole population in cool years. Under long-day conditions (17 to 18 h), nymphs develop slowly; they reach last instar and molt to adults at the end of the summer when day-length decreases. The mechanism of qualitative PhPR turns on, determining the onset of a facultative adult diapause and ensuring safe and successful overwintering.

The second, bivoltine, type of seasonal development is realized by specimens hatching from eggs laid earlier in the season, and is more typical of warm years. In this case, nymphs meet with short-day conditions twice during the season—in spring and in autumn. This accelerates growth significantly and increases chances for successful completion of the life cycle. Bugs of the first generation complete nymphal development and mature as adults under long-day conditions; this determines their reproductive activity. At the end of the vegetative season, the decrease of both ambient temperature and day-length induces diapause in almost all bugs of the population.

If bugs get into intermediate conditions, both active and diapausing fractions are formed, that is, both types of seasonal cycles are realized simultaneously (Saulich *et al*., 1993; Saulich *et al*., 1994).

Saunders (1983) understands the role of quantitative PhPR in the control of univoltinism in the Bohemian population of *P. apterus* in a similar way. He treats retardation of nymphal development as "a natural phenomenon with a real regulatory function and selective advantage," which could serve "to tighten up the scatter of physiological ages among nymphs, and thus encourage univoltinism in the population as a whole" (p.404) by synchronizing the emergence of adults.

A. custos, E. lewisi, and *E. oleracea*. In these three species, the role of photoperiodic control of nymphal development is probably not of critical importance. However, it may be assumed that the quantitative PhPR inducing retardation of nymphal growth under long-day conditions participates in adult emergence synchronization. This allows nymphs hatched from late eggs and living under the cooler conditions of the beginning of the autumn to complete their development successfully.

The Univoltine Species

The role of the photoperiodically induced retardation of nymphal development in the majority of the species studied is likely to be limited by the synchronization of adult emergence. In this way, we can understand the results of our experiments with *P. prasina* and *C. marginatus.*

P. angulosa is a polyphagous heteropteran with an obligatory adult winter diapause, poor ability to select oviposition-site, and long oviposition period (Hori, 1986, 1988). Without short-day acceleration of nymphal development, nymphs hatched late in the season or from eggs placed on unsuitable plants would grow too slowly. Emergence of adults would be retarded, and these adults would not be able to accumulate enough food reserve for overwintering and reproduction in the next spring. Adaptation in the form of a synchronizing effect of short and decreasing day-length on the nymphal development allows them to avoid this situation. Ultimately, the earlier in the season nymphs hatch out, the more slowly they grow (Hori, 1986, 1987).

C. humerigera. The seasonal cycle of this species is complicated. It includes two facultative diapauses: winter nymphal and summer adult (Kiritani, 1985a, 1985b). The nymphal diapause manifests itself as a retardation of nymphal development induced by short and decreasing day-length (see above). Nymphs can terminate diapause and resume active development already by the winter solstice, but they remain dormant because of the low temperature. The increase of both day-length and ambient temperature in the spring stimulates nymphal development and synchronizes the emergence of adults (Kiritani, 1985b). It is precisely this increasing day-length which induces an adult diapause resulting in the extension of the preoviposition period. Oviposition begins after the summer solstice when day-length decreases. Moreover, all females—both emerged earlier and later in the season—begin oviposition synchronously. This mechanism of oviposition triggering is considered to be an adaptation which allows nymphs to avoid the long-day part of the season and ensure formation of winter diapause the off-spring (Kiritani, 1985a).

To conclude, the qualitative and quantitative PhPRs are of great ecological importance. Both of these control the seasonal development. The qualitative PhPR dominates in the induction of winter dormancy. The quantitative PhPR, which controls rates of nymphal development, is more important for synchronization of the dormant and active stages with the most suitable terms in the season.

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